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IMPACT OF FLORAL ORIGIN, FLORAL COMPOSITION AND STRUCTURAL FRAGMENTATION ON BREEDING SUCCESS IN BLUE TITS (*CYANISTES CAERULEUS)* AND GREAT TITS (*PARUS MAJOR*)

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A Thesis in partial fulfilment of the requirements of Anglia Ruskin University for the degree of Doctor of Philosophy

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ABSTRACT

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IMPACT OF FLORAL ORIGIN, FLORAL COMPOSITION AND STRUCTURAL FRAGMENTATION ON BREEDING SUCCESS IN BLUE TITS (*CYANISTES CAERULEUS*) AND GREAT TITS (*PARUS MAJOR*)

By JULIA MACKENZIE

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Existing research on the foraging ecology and breeding biology of blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) has mainly concentrated on populations in woodland. However increasing urbanisation means much of the suitable tit habitat is represented by fragmented areas, not large woodlands, and little is known about factors that may affect reproductive success in urban environments. Using General and Generalised Linear Models this study compared reproductive performance in four habitat types with differing levels of habitat modification: the Cambridge University Botanic Garden (CUBG) with an abundance of non-native vegetation and structural fragmentation, two marginal sites with native scrubby vegetation and structural fragmentation and small fragments and large fragments of native woodland. Compositional analysis was used in a study focused on how foraging blue tits used the heterogeneous habitat of the CUBG. Additionally frequency tests were used to compare foraging preferences and foraging behaviours of both species in the CUBG.

Productivity was poor in the CUBG compared to all of the other habitats, with great tits appearing to do worse than blue tits, rearing lower quality chicks (significantly lower mean mass than in other habitats). Within the CUBG, positive relationships were found between the abundance of native trees and shrubs and breeding success for both blue tits and great tits. A positive relationship was found between breeding success in blue tits and the abundance of *Quercus* and *Betula*. However, habitat and year interactions showed that habitat and reproductive relationships were complicated by annual variation. The two species differed in their foraging preferences in the CUBG; blue tits were observed feeding in native deciduous trees significantly more than in non-native species and had a preference for birch trees over other taxa. Great tits however showed no strong preferences for any of the habitat types. With regards to foraging behaviours, great tits used a wider range of foraging heights and different foraging locations and capture techniques than blue tits. Blue tits were observed 'hanging' from twigs more frequently, and appeared to be more effective at foraging in the wider variety of plants available in the heterogeneous vegetation of the garden. The data presented in this thesis suggest that blue tits have adopted a better foraging strategy by preferentially choosing native deciduous trees over the abundance of non-natives available in the CUBG. However, despite the apparent better foraging strategy of blue tits, reproductive performance of both species is poor in this urban garden compared to marginal sites and woodland. Urbanisation and the associated loss of optimal tit habitat are likely to continue. It is therefore important to offset urbanisation by the addition of appropriate foraging habitats that are likely to improve reproductive success, such as native trees and shrubs.

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CHAPTER 1

General introduction

1.1 Thesis aims and objectives

Since the middle of the twentieth century there has been a vast amount of research on the ecology of blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) breeding in oak woodland habitat (Dhondt, 1987, 1989; Kluijver, 1951; Lack 1947, 1955, 1958, 1966; Perrins, 1965, 1970, 1979, 1991; Perrins and Moss 1975; Wilkin *et al*. 2009). This wealth of research has been important to the development of natural history theory, covered by many ecological text books (e.g. Begon *et al.* 2006; Ricklefs and Miller 2000), that argues breeding in birds is shaped by natural selection to maximise lifetime reproduction (fitness). Birds have evolved to, on average, time their breeding so that the peak demand for food by nestlings matches the peak supply of suitable food. Additionally, in their optimal habitat, birds have evolved to lay a clutch size that enables the maximum number of fledglings to be produced, appropriate to the food supply (Lack 1954). As they are adapted to optimal habitats, in poorer habitats their behaviour may be inappropriate. It has for example been shown that productivity of blue tits and great tits is low in fragmented woodlands and marginal habitats, with breeding performance poorest in urban environments such as parks and gardens (Cowie and Hinsley 1987; Hinsley *et al*. 2008, 2009). My work aims to test the factors that may affect reproductive success in urban environments, such as floral origin, floral composition and structural fragmentation. I aim to compare reproductive success in urban habitat with other habitats that have differing degrees of modification to habitat structure and floral composition. I also aim to explore how blue tits and great tits may differ inter-specifically in their responses to modified habitats. By understanding factors

which may optimise breeding in urban environments, recommendations can be made for future landscape management to increase bird breeding success and maintain populations. Not only could these conservation measures be applied to blue tits and great tits, but they would also be relevant to the majority of insectivorous woodland birds thus making a significant contribution to bird conservation in an urbanising world (Marzluff 2001; Balakrishnan 2007).

Specifically, reproductive performance will be compared at the following sites with differing habitats:

1. The Cambridge University Botanic Garden (CUBG), which is characterised by heterogeneous vegetation with an abundance of exotic trees and shrubs and structural gaps.
2. Wicken Fen and Cow Lane, which are marginal, fragmented habitats consisting of native trees and scrubby native flora but with many structural gaps, missing the canopy structure of woodland.
3. Small (c. 1 ha), fragmented native woodland patches.
4. Large (c. 150 ha) native woodland, optimal habitat for blue tits and great tits, to be used as a control against which to test the marginal habitats.

Additionally, my aim is to understand the consequences for breeding birds of the heterogeneous habitat of the CUBG and areas within it, by assessing tit foraging preferences and foraging behaviours during the breeding season, and relating these to breeding performance.

1.2 Avian Breeding Ecology

Avian breeding seasons represent an energetically demanding period when parent birds engage in numerous activities including nest building, egg laying and chick rearing. How these birds time their breeding (date of first egg) and their investment in reproduction (number of eggs laid) is of much interest to biologists. Understanding the underlying causes of timing and reproductive investment can tell us a great deal both about the evolutionary consequences of a particular behaviour (the ultimate or 'why-question' approach) and the physiological mechanisms mediating a behaviour (the proximate or 'how-question' approach) (Wehner 1997).

Ideally, the optimum clutch size for a breeding pair should maximise the number of their progeny surviving to breed and hence their genetic representation in the population (Lack 1947, 1954). Too large a clutch and the parent birds may struggle to feed their young and, in the worst case scenario, their chicks starve. Too small a clutch and a breeding pair have missed out on an opportunity to maximise their fitness. However, in practice, achieving this ultimate goal of leaving the most progeny is not straightforward and parent birds face constraints that impact their reproductive effort. The decisions that the parents make in response to these constraints can affect their fecundity and both their chance of survival and that of their progeny. Life history theory analyses these responses and how they have been shaped by natural selection. The following section will look at life history theory in more detail with an emphasis on its development.

1.3 Avian life history theory

An organism divides its time and energy between the various stages of its life, which includes its birth, growth to maturity, reproduction and death (Gill 2007; Purves *et al.*

1998). During its lifetime, a number of traits or characters are expressed by an individual such as size at birth, age at first reproduction and number of offspring produced. These traits differ both between and within species. For example, a small passerine such as a song sparrow (*Melospiza melodia*), which has a short lifespan, begins to breed when it is just a year old whereas a longer lived bird, such as a wandering albatross (*Diomedea exulans*), does not commence breeding until 8 to 11 years of age (Gill 2007). How does natural selection result in these observed differences? Life history theory suggests that life history strategies evolve which maximise an individual's survival and fecundity, i.e. which maximise lifetime reproductive success.

Life history theory has mainly focused on the phenotypic adaptation of individuals and how the environment shapes their behaviours (Daan and Tinbergen 1997) and it is most advanced in the analysis of reproductive decisions which affect the fitness of individuals. Fitness is the measurement of natural selection in terms of the number of surviving offspring left in the next generation (Raven *et al.* 2005).

1.3.1 Development of natural history theory

It was in fact early research on clutch size in birds which paved the way for the development of life history theory in all organisms. Clutch size was found to increase at higher latitudes both within and between species (Moreau 1944). This influenced the work of David Lack (Lack 1947, 1954, 1966) who developed the idea that clutch size has evolved through natural selection to enable parents to lay the biggest clutch that they can rear successfully and which leads to the greatest number of eventual adult survivors. He argued that the increase in clutch size at higher latitude was due to food supply - birds were able to forage for longer and therefore acquire more food in the

longer days of temperate regions as opposed to the shorter days within the tropics. Although other ideas were formulated to account for clutch size variation in birds, Lack's theory became the dominant thinking of the time. Figure 1.1 below summarises this theory and the reasons why Lack challenged and rejected other ideas that had been put forward (Lack 1954).

1) A bird lays as many eggs as it is physiologically capable of. Lack dismissed this saying that many passerines are capable of obtaining sufficient energy from food supplies to enable them to continue laying if eggs are taken away and which, if combined, would result in a total greater than the original clutch size.

2) The female lays as many eggs as she can adequately incubate and keep warm. Lack dismissed this saying there are often cases where birds lay a clutch larger than the average but that still hatches successfully.

3) Clutch size is adjusted through natural selection to balance the mortality of an individual species meaning that at very high population densities the clutch size would be reduced to prevent consequential overpopulation. Lack also rejects this saying that when populations are high clutches are not adjusted to an extent that would compensate for the consequential mortality from lack of food. It also suggests group selection - that individuals are acting for the good of the population - rather than natural selection which favours the individual genotype.

4) Clutch size has evolved through natural selection to enable parents to lay the biggest clutch that they can rear successfully and leads to the greatest number of eventual adult survivors. Lack's theory, which he supported by saying that birds struggle to feed larger than average broods, despite the parents bringing more food (the food increase is not proportional to the brood increase so the chicks receive relatively fewer feeds). Lack uses a number of examples including the observation that in great tits the young from larger broods weigh less than those in smaller ones and that heavier nestlings were the most likely to survive post-fledging.

Figure 1.1 Lack's (1954) rejection of alternative theories explaining the evolution of clutch size (points 1-3) and his own theory (point 4).

Lack's theory was concerned with the maximum number of offspring that could be produced in just one breeding attempt. Williams (1966) proposed that clutch sizes reflected the maximum number of offspring an individual could produce over its lifetime as opposed to just one reproductive bout. He argued that birds faced costs in

reproducing due to adult survival decreasing with increasing reproductive effort (measured by clutch size) since the extra energy used by the parent bird in raising a large clutch could result in its own death. This would prevent future reproductive attempts and ultimately lead to lowered overall fecundity. Williams (1966) therefore advanced the idea that decisions about how much investment parent birds should make in one reproductive attempt could have either positive (increased fecundity) or negative (increased parental mortality) consequences for future attempts. In life history terms a change in strategy and its consequences became known as a trade-off (Daan and Tinbergen 1997).

Another hypothesis accounting for clutch size variation emerged from Perrins and Moss (1975), who argued that when taking all factors into consideration, the most productive brood size (i.e. the one which produces the most surviving young) is usually the natural clutch size (i.e. not a manipulated larger or smaller clutch). This led to the development of the Individual Optimization Hypothesis (IOH) (Pettifor *et al.* 1988) derived from Lack's theory. They argued that an individual lays a certain number of eggs which will result in the maximum number of recruits (offspring reproducing in the following season). In their study of great tits (Pettifor *et al*. 1988), they found no evidence that parents raising an artificially enlarged brood suffered a higher mortality or lower fecundity and so argued against Williams' (1966) hypothesis. The IOH was a refined version of Lack's theory since Lack had previously argued that the peak demand of the nestlings coincided with the peak supply of food and so meant that the average bird in a population should be the one raising the most offspring. However population studies (e.g. Kluijver 1951; Perrins 1965) showed that it was earlier breeders that were the most successful, having the largest clutches and highest numbers of surviving young, suggesting that the average individual in the population was behaving sub-optimally. The IOH took into account clutch size variation throughout the season by arguing that

the differential success through the breeding season represented differences in individuals in their abilities to raise offspring and therefore reflected differences in the optimal clutch size for each bird as opposed to the population average.

Both the Cost of Reproduction (or Trade-Off) hypothesis and the IOH have become key hypotheses in life history theory and helped to shape key concepts such as parental investment, trade-offs (previously discussed) and optimization. Optimization uses modelling to determine which particular trait or traits are 'optimal' (i.e. which maximise fitness) for individuals under particular environmental conditions (Daan and Tinbergen 1997). As in the IOH, the traits which maximise fitness may be different for each individual within a population.

More recent studies have tested these hypotheses and concepts. Pettifor *et al.* (2001) for example repeated their 1988 study on great tits using a data set for a greater number of years. The findings were still the same; recruitment was greatest for parents rearing a brood size equal to their own natural clutch size (i.e. a brood that had not been experimentally increased or decreased). Additionally, they found that birds laying naturally larger clutches were of greater fitness, in terms of recruitment, than birds laying naturally smaller clutches.

To test for parental investment and future survival of both parents and their offspring these studies often involve experimental manipulations and usually involve encouraging parents to alter their expenditure in parental activities in some way. For example, flight feathers of great tits have been clipped (thus handicapping them by increasing flight costs) to assess parental investment in birds with bi-parental care (Sanz *et al.* 2000). This experiment showed that handicapped males suffered more than females in terms of their (hypothesised) survival from the increased effort in feeding young. However,

increasing brood size is still the favoured manipulation to test trade offs between offspring condition and parental investment. For example, in barn swallows (*Hirundo rustica*) an experimentally increased brood size has been shown to result in reduced survival of parents (Saino *et al.* 1999). Saino *et al.* (1999) also found that male parents suffered lower survival if their offspring had higher immunocompetence suggesting competition between the nestlings and parents to gain the nutrition needed to increase immune function, i.e. empirical evidence of a parent/offspring trade-off. Other costs of increased parental effort have been shown in eastern bluebirds (*Sialia sialis*) where males grew duller plumage in the breeding season following increased feeding effort manipulated by brood enlargement (Siefferman and Hill 2005). Conversely, males who had a reduced brood size were able to produce brighter plumage the following breeding season allowing them to attract better quality females who laid eggs earlier in the season.

Direct measurements of parental effort are now possible. The daily energy expenditure (DEE) of parent birds can be calculated using techniques such as doubly labelled water (DLW), in which the average metabolic rate of an organism is measured over a period of time (Speakman 1997). Studies have shown that in small birds such as marsh tits (*Poecile palustris*), DEE increases in response to increased clutch sizes due to increased parental feeding effort (e.g. Nilsson 2002) and DEE also increases due to low quality patchy habitat, where birds such as great tits often have to travel large distances between patches and search for longer to find invertebrate food (e.g. Hinsley *et al.* 2008). These studies address the constraints which can shape life history or in some cases show sub-optimal behaviour. Engstrand *et al.* (2002) suggested that "the greater likelihood of raised energy expenditure associated with larger clutches, combined with the difficulties in maintaining energy supplies, may constitute a constraint on avian clutch size".

1.3.2 Brood size and food limitation

Extensive work on blue tits by Blondel and his colleagues, including experiments involving brood manipulations, suggests that not all breeding behaviour is adaptive (e.g. Blondel *et al.* 1993, 1998). They compared populations on the mainland of France to populations on the island of Corsica in two habitat types, preferred deciduous habitats and evergreen habitats which have a lower abundance and variable supply of invertebrate food (Blondel *et al.* 1993). Clutch sizes were 27% smaller on Corsica than on the mainland (Blondel *et al.* 1987) yet experimental brood reduction on the island in evergreen forest showed that the recruits the following breeding season were of higher quality (higher fledging mass and longer tarsus), and had a greater potential to lay more eggs than recruits from an enlarged clutch or a control clutch (Blondel *et al.* 1998). Blondel *et al.* (1998) argued that this showed that the normal (mainland) clutch size was maladaptive for the island evergreen habitat and needed to be reduced in order to become optimal. Their study therefore found that clutches on Corsica did not fit the IOH nor did they find any costs of reproduction to the parents (Blondel *et al.* 1998). It is possible that the birds on the island are unable to evolve an adaptive clutch size due to the continual influx of individuals from the mainland (Blondel *et al.* 1993).

Lack's theory (Lack 1947, 1954, 1966) suggested that food supply was the main cause of clutch size variation, but food limitation as a cause of clutch size variation has been criticised by Martin (2004). Martin (2004) argued that brood manipulations test only proximate responses and therefore fail to establish if food limitation is the ultimate, evolutionary cause of clutch size variation.

Food limitation has also been studied in relation to the timing of birds breeding season. Perrins (1970) hypothesised that food supply is a proximate constraint on the female.

He found that in birds such as the great tit and the Manx shearwater (*Puffinus puffinus*) most individual birds laid too late for the offspring to make full use of the peak abundance of food. He argued that the female would ideally lay her clutch earlier since earlier laying led to greater numbers of surviving young, but that the food needed for egg production was in short supply early in the season and so constrained early laying. This led to direct testing of (what became known as) the food constraint hypothesis. By supplying supplementary foods in the field, studies have shown that individuals receiving food did lay earlier, supporting Perrins (1970) hypothesis (see review in Martin 1987). However, many of these early studies resulted in very small advances in laying date thus suggesting that other factors than food supply were involved in timing of breeding. They also did not test timing of breeding in a life history context (Drent 2006).

Food supplementation experiments have therefore been taken further and one study (Gienapp and Visser 2006) has assessed adaptations to local environments. This study found that great tits can learn to 'fine tune' their laying dates in the following year; females which were experimentally exposed to an artificial food peak (an abundance of meal worms provided once laying had started) suggesting they had bred too late, would breed significantly earlier in the following year (Gienapp and Visser 2006). Another recent study has found that the effects of supplementary food depended on the natural resource level, with only blue tits in food-poor habitats advancing their laying dates with the addition of supplements (Bourgault *et al*. 2009)

Brinkhoff *et al.* (2002) manipulated the timing of breeding of European coots (*Fulica atra*) by exchanging (first) clutches that differed by 10 days in laying date but were of equal size. They discovered that parents in the advanced laying group had a greater mortality rate than those of the delayed group, but the latter had a lower probability of

having a second brood and therefore a reduced overall output. This suggested that in this species there is a cost associated with laying early and that parents face a trade off between their own mortality and having a higher output of young. Thus the natural date of laying may represent the optimal solution for specific individuals. Brinkhoff e*t al.* (2002) and Drent (2006) argued that this study was supportive of the IOH, which in this case was used to explain variation in timing of breeding instead of clutch size (as discussed above).

1.3.3 Variation between individuals

A new focus of study in behavioural ecology has been to understand phenotypic variation in personalities of birds which could help to reveal why individuals adopt differing strategies and assess whether different personalities have consequences for fitness. Dingemanse *et al.* (2002) studied exploratory behaviour in wild caught great tits in a laboratory environment with five artificial wooden trees and found that their behaviour was heritable meaning that traits from individual personalities are subject to natural selection. In great tits speed of exploratory behaviour is positively correlated with aggressiveness, boldness and risk-taking (see review in Dingemanse and Réale 2005). They went on to study the consequences that different personalities may have on fitness and found that adult survival fluctuated between years and was in each year opposite for males and females so that slow-exploring males and fast exploring females had better survival in some years but that fast-exploring males and slow-exploring females had better survival in others (Dingemanse *et al.* 2004). This was argued to be related to fluctuating food supply of beech mast in winter; in poor years females, which are subordinate to males (Dingemanse and de Goede 2004) survived better if they had fast exploring personalities. They would be more aggressive to other females and could thus out-compete them for food, whereas males in poor years survived better if they had

slow-exploratory personalities since less food in winter meant less recruitment in spring due to higher mortality in winter. As a result competition for territories in spring is relaxed so there is no need for overt aggressiveness (Dingemanse *et al.* 2004), which can incur costs. The personalities of parents was also related to offspring success with slow-exploring females having better reproductive success, producing more and larger offspring than fast-exploring females (Both *et al.* 2005). Both *et al.* (2005) hypothesised that fast-exploring individuals are better able to defend and obtain high quality territories and thus this represents a trade-off between being a better parent (slow-explorer) or gaining a better territory (fast-explorer). These studies show that there are both costs and benefits in having the differing personalities and that environmental factors may influence the best behavioural traits for both survival and reproductive output.

Life history theory has been explored in this section and has shown that certain heritable traits of an individual interact with the environment to determine lifetime reproductive success. Many individuals differ in these interactions and these differences are sometimes adaptive but can be maladaptive. In the next sections I will look more specifically at the factors influencing the timing of breeding, clutch and brood size and offspring survival, including both proximate and ultimate factors and constraints.

1.4 Factors affecting timing of breeding

The time at which birds lay their eggs has been shaped by natural selection to coincide with the time in which the food is most abundant for their nestlings (Lack 1947; Perrins 1965, 1996). Thus breeding must begin much earlier than peak food availability because a period of at least three weeks must elapse to allow egg laying and incubation (the shortest period found in birds) (Perrins 1970; Cichon and Lindén 1995). Birds cannot

"know" exactly when the peak abundance of food is likely to occur so how do they know when to commence breeding?

1.4.1 Photoperiod

Changes in photoperiod provide a reliable general indication of the timing of the seasons in temperate latitudes. The increase in day length in late winter and early spring is the main proximate factor that dictates the general date of laying in most birds in temperate and cold climates (Dawson *et al.* 2001; Kluijver 1951; Perrins and Birkhead 1983). Changes in day length stimulate hormonal responses which promote gonadal growth and maturation (Phillips *et al.* 1985; Dawson *et al.* 2001; Dawson and Sharp 2007). Thus, with the physiological capability to breed under hormonal control in response to photoperiod, it might be expected that all individuals of a species could lay within days of each other. However there is considerable variation within populations; in practice, laying dates can vary by weeks in passerines. Although photoperiod is the factor which determines the window when breeding is physiologically possibly, other proximate cues and constraints on individuals affect the exact breeding date (Perrins 1965).

1.4.2 Food supply

The female may be constrained by her ability to collect food prior to egg laying. This is shown in small passerines, which often lay large clutches at a rate of one egg per day. The amount of surplus food that is required for energy to produce eggs, and the calcium needed to produce thick enough egg shell, is great (Perrins 1996; Carey 1996) and the need occurs before the peak abundance of food. This problem may be exacerbated in temperate areas where food may be scarce at the end of the winter (Perrins 1970;

Siriwardena *et al* 2008) and the food that is available may be poor in quality in relation to the needs of egg formation (Blondel *et al.* 1987). A female must consequently delay breeding until there is sufficient food available of a quality to enable laying and this could mean the peak abundance of food may have passed when she has her young in her nest. Therefore, the earlier a pair can commence breeding the more successful they are likely to be in leaving the most surviving progeny. This has been shown in species such as the great tit (and to a lesser extent the blue tit), where intensive long term studies have been conducted in Holland (e.g. Kluijver 1951) and Britain (e.g. Lack 1954). This is also similar in other species of small insectivorous passerines such as the pied flycatcher (*Ficedula hypoleuca*) (Lack 1966) and non-passerines such as the Manx shearwater (Perrins 1970).

Supplementary feeding experiments in some birds have also demonstrated the importance of food supply to females prior to laying (see review in Perrins and Birkhead 1983). However, in high-quality territories, for the blue tit, this effect is not pronounced and early laying is possibly due to other cues (Svensson and Nilsson 1995). Similarly, laying date may not be affected at all by supplemental food as shown in the Nazca booby (*Sula granti*) (e.g. Clifford and Anderson 2001). Thus egg laying may only be advanced to a limited extent by food supply (Martin 1987) or not at all.

1.4.3 Age

The age of a female has also been demonstrated to affect laying date, with those breeding for the first time generally laying later than older birds within a population (Perrins 1970). Perrins (1970) suggested that this was most likely due to younger birds being inexperienced and unable to successfully increase their foraging effort to get into good breeding condition early. Kluijver (1951) suggested that in great tits heritable

differences may dictate whether individuals lay a few weeks early or later than the average within a season, more so than environmental cues or age. Blondel *et al.* (1987) have observed a constancy of laying date from year to year in the same individual blue tits.

1.4.4 Temperature

Between years, laying date is subject to change due to fluctuations in spring temperatures and this can be seen in the pied flycatcher and great tit where warmer temperatures in March and April lead to earlier laying (Lack 1966). Previously, Lack (1954; 1958) believed that these birds may have evolved an 'anticipatory' adaptation to know when the most food would be available for the chicks. For example, warmer temperatures could be used as an indication that breeding should begin earlier to coincide with the caterpillar food that would emerge earlier in warm conditions. This assumed that birds such as great tits and pied flycatchers have a prior knowledge of caterpillar population dynamics, which is unlikely to be true and Lack (1966) later accepted the modified view of Perrins (1965). Perrins believed that the real reason that laying is earlier in warmer springs is due to the warmth causing an earlier emergence of insect food needed by the females to form their eggs and which therefore allowed her to get into breeding condition earlier. However, the exact reason for earlier laying in warmer springs is still disputed today. Nilsson and Källander (2006) compared sites in differing climates and the warmer climate lead to earlier budburst on the trees and earlier laying in great tits and blue tits. They argued that budburst is used as one of the cues to indicate to the tits when caterpillars will emerge on the trees, which would be earlier in the earlier bud burst.

1.4.5 Habitat

A final factor that influences timing of laying within species is habitat type and structure; often the same species will breed at slightly different times depending on the surrounding vegetation (Perrins and Birkhead 1983). Usually earlier breeding will occur in the habitat with the richest food supply for a particular species and this can be seen in the extensively studied great tit. In Corsican pines for example, laying dates are often very late in a season when compared to an English broad-leaved wood and Lack (1955) puts this down to poor insect availability in the former rather than other factors such as climate. However, a problem occurs with great tit laying dates in gardens as this is usually earlier than in any other habitat type (Dhondt *et al*. 1984), yet gardens are often poor breeding areas, with many nestlings starving (Perrins 1965; Chamberlain *et al*. 2009). The same early breeding has been found to be true for blackbirds (*Turdus merula*) in the Oxford Botanic Garden where food for nestlings is also poor (Lack 1966). How then can the argument hold that earlier breeding occurs in the 'best' habitat when gardens are so obviously poor?

Various hypotheses have been put forward to attempt to explain this phenomenon although notably the issue still remains unresolved. Some authors have for example, suggested that supplementary food put out by people in gardens over winter results in earlier laying dates (Chamberlain *et al*. 2009; Kluijver 1951). Perrins (1965) on the other hand believed that although the caterpillar abundance may be poor for chick rearing, the availability of a variety of small invertebrates prior to egg laying may be good and allow the female to get into breeding condition earlier. Warmer temperatures in urban areas and greater light intensity due to more open habitat and artificial lighting, potentially resulting in buds/leaves emerging earlier and consequentially earlier insect

emergence, have also been offered as potential explanations for earlier laying in gardens (Lack 1958).

Summarizing, it has been argued that ultimately birds have evolved their breeding season and laying dates to coincide with peak availability of food for their nestlings and that photoperiod is a reliable proximate cue to indicate the window in which reproduction can occur. Many birds however are not able to lay at the most opportune time and this is due to constraints such as food availability prior to laying, spring temperature, age of female and habitat type.

1.5 Factors affecting clutch size

1.5.1 Time of breeding

It must be stressed before embarking on a review of other factors affecting clutch size that clutch size and timing of laying are not mutually exclusive aspects of breeding, despite being dealt with separately here. Before considering other factors affecting clutch size I will firstly deal with interactions between these two. In many birds, clutch size varies throughout the season and a common occurrence is for the latest breeders to lay the smallest clutches (e.g. Perrins 1965; Lack 1954). This is thought to be in response to the passing of the peak food availability for the nestlings and thus an adaptation to the worsening food supply for these nestlings (Perrins and Birkhead 1983). Birds that lay later in the season lay smaller clutches at a time when the food supply is likely to be at or near its maximum, which shows that food supply is not the (only) factor controlling clutch size (Kluijver 1951; Lack 1954; Perrins 1979). Single- and multi-brooded species differ in their clutch size patterns, possibly representing adaptations to the specific food supply of each individual species, with single brooded

species (e.g. great tit in the UK) having a progressive decline over the season and multi-brooded species (e.g. yellowhammer, *Emberiza citrinella*) having a clutch size that rises from April to June and then declines (Lack 1954). However, if multi-brooded species lay late in the season the pattern seen in the clutch size of single-brooded species may occur (Gil-Delgado *et al.* 2005).

1.5.2 Age

In a wide variety of birds, those breeding for the first time often have smaller clutches than older birds, even when taking into account the effect of earlier laying by older birds (Kluijver 1951; Lack 1954; Perrins 1965; Perrins and Birkhead 1983). This may represent a constraint, reflecting an inability of young birds to find food and produce a full sized clutch. However, it has been suggested that this is an adaptation, reflecting their relative lack of experience and lower efficiency as parents than older birds (Lack 1966). This is convincing in great tit studies where proportionately more chicks survive if raised by older-than-yearling parents (Perrins 1965). Thus having a smaller clutch and therefore smaller brood may represent an adaptation permitting young, inexperienced parents to raise the maximum number of surviving chicks (Lack 1966).

1.5.3 Population density

Studies in great tits have shown a negative correlation between population density and clutch size (e.g. Kluijver 1951; Lack 1958; Perrins 1965; Both 1998). This effect has been related to food supply in that food would be in greater demand when population size is large and its abundance may be too low to support large clutches/broods (Perrins and Birkhead 1983). Territories are also smaller at high densities and Kluijver (1951) argued that in very dense populations birds may not breed at all due more to territorial

disputes than food availability. Lack (1958) suggested that large populations of great tits generally contained large numbers of yearlings and hence clutch size variation could be associated with their laying of smaller clutches. However, he also recognised that territorial disputes and depletion of food were probably the main factors involved.

1.5.4 Weather

Cold weather can cause females to postpone egg laying or, if the bird has already begun to lay, cause her to lay a smaller clutch than would otherwise have been the case (Perrins 1965). Perrins (1965) believed that in great tits this phenomenon was due to insects becoming less active in cold weather and therefore more difficult to find resulting in female breeding condition being impaired by this loss of foraging opportunity

Speculatively, Lack (1954) suggested that other weather factors that vary seasonally, such as rainfall or hours of daylight, might cause clutch sizes to vary in birds, and in semiarid regions rainfall may be an important factor. For example, Illera and Díaz (2006) found smaller clutches in drier years in Furteventura in the Canary Islands stonechat (*Saxicola dacotiae*). However, Kluijver (1951) found no affect of weather or temperature on clutch sizes in great tits in Holland and so the extent to which the weather affects clutch size in more temperate areas is probably minimal. Rainfall may therefore be a more relevant factor affecting clutch sizes in tropical or semi-tropical areas, which are affected by annual rainy seasons.

1.5.5 Habitat

Birds of the same species often lay different sized clutches in different habitats, even when other factors such as population density are taken into consideration (Perrins 1965). It has been thought that the clutch size of an individual species will be the largest in the habitat in which the species is commonest and to which it is specialised (Lack 1958). This phenomenon has been studied in tits due to variability in their clutch sizes in different habitats - that of the great tit can vary between 5 and 16 eggs (Kluijver 1951). For example in blue tits, which are described as oak specialists, their clutch is the largest in pure oak than in mixed woodlands and smallest in pines (Lack 1958; Perrins 1965). In great tits, which do not have such a preference for oak over other broad-leaved trees, their clutch is larger in so called 'good woodland' (larger and more densely packed trees) than 'poor woodland' (Perrins 1965) and slightly lower in pine than in deciduous woods (Kluijver 1951). Note however, that in England, birds breeding in Scots pine were found to have similar clutch sizes as in deciduous woodland (Lack 1958), and I will come back to this point later. Additionally, it was understood early in the investigation of life history theory by Kluijver (1951), Lack (1954) and Perrins (1965) that females inherit the ability to vary their clutch sizes within their own individual genotypic limits and that they can modify their clutch according to environmental conditions within years. So a female who lays an above average clutch in say a 'good' habitat would have a smaller clutch size in a 'bad' habitat but this smaller clutch would still be above average size in this 'bad' habitat (Perrins 1965).

Both species were found to have smaller clutches in garden habitats (Cowie and Hinsley, 1987; Kluijver 1951; Lack 1958; Perrins 1965). It has been argued that these variations are due to the tits adapting to their environment by laying the most productive clutch in order to leave the most surviving young and that this is again related to food

supply (Perrins 1965). Perrins (1965) argued that since tits (probably) cannot predict caterpillar abundance in certain habitats, they are probably going by habitat appearance and structure to predict the potential food supply. So in gardens for example, the structural cues of interrupted leaf canopy (rather than closed leaf canopy as in woods) could be indicative of providing fewer caterpillars and therefore a smaller clutch size would be needed in order to prevent starvation of nestlings (Lack 1958). However, It is somewhat paradoxical that urban tits have an inhibited clutch but are often found to lay earlier in urban environments, when early laying has been related to good quality food supply and habitat (see section 1.4).

The fact that young in gardens were found to have a high mortality rate, despite the tits adjusting their clutch size downwards (Cowie and Hinsley 1987; Perrins 1965) suggests that this adaptation does not always work and that the clutch produced is still over-ambitious. Lack (1958) suggested that maladaptations such as this may happen due to gene flow preventing the evolution of a local response appropriate to the food supply. This could also be why great tit clutch size in Scots pine does not differ from that in deciduous woodland despite the difficulty of finding enough food in the pine (Lack 1958).

1.5.6 Food supply

Lack (1966) argued that most of the factors discussed above that affect variation in clutch size are often indirectly associated with the food supply available for the brood. The birds use habitat type, population density and cold weather as indicators of future food supply. Supporting this theory is evidence from the great tit where clutch size has been found to be correlated with the numbers of caterpillars in the season (e.g. Perrins 1991). Caterpillar development can be highly variable, growth rate being affected by

temperature which, in very warm spells, can rapidly increase development and pupation (Perrins 1991). Thus it would make sense that clutch size can be varied in parallel with caterpillar abundance, but with the caveat that increased caterpillar development does not shorten availability during the nestling period.

1.6 Factors affecting offspring survival

Mortality once nestlings actually leave the nest is generally very high in the first few weeks for tits (but cf. Dhondt 1979). In Wytham Woods in winter there can be as few as one juvenile great tit to every six older birds and the survival of young to the next breeding season has been estimated at 22% (Perrins and Birkhead 1983). Small passerine survival does however vary amongst individuals. In general, those having a good state of physical development when they leave the nest are more likely to survive (survival being measured by the number of future recaptures) (Davies 1986; Dhondt 1979; Gill 2007). The factors that affect a fledgling's physical condition, and therefore their likelihood of survival, are reviewed below and since a large amount of work has been conducted on tit species (Paridae), most of the following examples will be from this family.

Most of the factors affecting the survival of chicks and fledglings are influenced by the availability of food and its quality and these effects can be seen in all periods of the breeding season, i.e. pre-laying, nestling provisioning and fledging. In the pre-laying period for instance studies have shown that increases in egg quality and size, which are influenced by food supply and quality (Martin 1987), have promoted increases in chick growth and survival in some avian species. For example, supplementary feeding during pre-laying and nestling periods of Florida scrub-jays (*Aphelocoma coerulescens*) may have improved survival of the chicks (Reynolds *et al.* 2003), and Rutkowska and

Cichoń (2005) have shown that a higher egg mass can lead to a higher survival probability in zebra finches (*Taeniopygia guttata*).

During nestling provisioning, Lack (1958) argued that poor food availability in certain habitats resulted in the poorer survival of great tits and blue tits. For example, he found that in broad-leaved woods over 95% of young blue tits and great tits were successfully raised to fledging, yet in pine woodland, only between 60-70% were successful. Poor food availability may also result in parent birds travelling further to find food, therefore increasing forging time and consequently decreasing rate of food provisioning (Lack 1958; Tremblay *et al*. 2005). However, other authors have argued that high feeding rates may reflect low quality habitat with low quality food being delivered to offspring (Mägi *et al*. 2009). Other studies have found that foraging rates may not differ between habitats, but that high quality habitats may have greater fledging success (Stauss *et al*. 2005). Differences in results across such studies may also be affected by interactions of prey load sizes, prey quality and feeding rates. Higher nestling mortality has also been found in gardens in blue tits and great tits due to starvation (Cowie and Hinsley 1987; Lack 1955; Perrins 1979) and Lack (1955) argued that additional human disturbance may have even more of a detrimental effect on future survival.

Nestling provisioning in great tits also varies according to the size of the brood, with a larger brood receiving more visits than a smaller one. However, this was found not to be a proportional increase to the number of young so a chick in a smaller brood will still receive more feeds per day (Gibb 1955; Kluijver 1951). This does not seem to create greater mortality in large tit broods in good woodland habitat and in fact smaller broods may not survive due to being more prone to cold (Kluijver 1951). If however, a large brood was late in the breeding season (or even a second small brood) then the feeding rate was found to decrease (Gibb 1955), and in English deciduous woodlands, late

repeat and second broods are prone to starvation (Lack 1966). This is probably due to the difficulty the parents find in foraging, due to decreased caterpillar abundance later in the season, with lower quality food, such as adult insects, often being used as a substitute (Lack 1966).

Early season great tit chicks in deciduous woodland therefore have a greater likelihood of survival than later ones and the greater nestling mass that is found in these early chicks is indicative of their future survival (Perrins 1965). Heavier young carry greater fat stores and are more likely to survive than lighter young. Fat would also help chicks survive on cold nights. Even later chicks that weighed the same than earlier ones were still more likely to die (Perrins 1965), which again could be indicative of a lower quality food supply later in the season. Late chicks may also be at a competitive disadvantage compared to older more experienced juveniles. However in different habitats, for example in pine, weights of nestling coal tits (*Parus ater*) and great tits are found to be heavier later in the season (Gibb and Betts 1963). Gibb and Betts (1963) argued that this phenomenon was reflective of the fact that the food supply was the main cause of the weight difference. In broadleaved woods the caterpillar supply decreases in the course of a tit's breeding season, whereas in pine it steadily increases resulting in a greater abundance of caterpillar food later in the season in pine.

On fledging, chicks raised earlier in the season also have an advantage over later ones as caterpillar numbers will still be fairly abundant (Perrins 1965). However by the time later chicks fledge this caterpillar abundance would have been severely depleted making foraging harder, which would be critical to their survival in the first few days of fledging, despite continued parental care. Also, since the later chicks are generally lighter, the lack of food may be exacerbated by their lack of reserves and it has been shown that more lighter than heavier young die (Perrins 1979). Although chicks do not

survive as well in gardens, Perrins (1965) argued that fledglings may do better than in woodland because, despite having very low weights, the conditions in gardens may be such that a greater food supply is available for longer. Garden fledglings may also benefit from artificial food supplies.

Kluijver (1951) found that in great tits the actual number of young fledging (production rate) is influenced by population density; at high population density low production rates were found and visa versa. Similarly, Both (1998) found that brood size and nestling mass were lower in great tits in (experimentally manipulated) high density plots and, although no effect was found for nestling survival, the nestlings were found to be of a lower quality. Both (1998) argued that being of low quality may have detrimental consequences for their future lifetime reproductive success and recruitment. Again the influence of population density on offspring survival is attributed to food supply and its faster depletion due to increased competition for food between the greater numbers of individuals (Kluijver 1951; Perrins 1965; Both 1998).

1.7 Outline of thesis

This chapter has provided an overview of the wealth of literature surrounding avian breeding ecology and the factors that affect reproductive success, and the historical importance of the research on blue tits and great tits. The following chapters will assess foraging preferences of blue tits and great tits in the CUBG (chapter three), compare breeding success across different habitats (chapter four) and assess foraging behaviours and techniques in the CUBG (chapter five). Conclusions (chapter six) will then be made in the context of this chapter, exploring the ability of blue tits and great tits to adapt (or not) to urban environments.

CHAPTER 2

Main site description

2.1 Methods

2.1.1 Main site

The Cambridge University Botanic Garden (CUBG) is a large urban landscaped garden (~16.5 ha) situated less than a mile to the south of Cambridge city centre (52° 12' N, 0° 08'E). It contains a mixture of over 10,000 labelled plant species (Cambridge University Botanic Garden 2005) with a variety of different origins, as well as cultivated varieties of 'garden origin'. Approximately 80% of the garden habitat was surveyed, excluding the lake and garden at the Bateman Street entry end (see Chapter 3, methods section *3.2.2*, for a detailed description of survey methods). The survey showed that 14.0% of the garden was composed of native trees and shrubs and 27.4% was composed of non-native trees and shrubs. The remaining garden was made up of herbaceous layers (26.2%), gaps (defined as the absence of any trees, shrubs, herbaceous layers, planted beds or hedges) (23.8%) and planted beds and hedges (8.6%). Figure 2.1 shows the locations of the 42 nest boxes in the CUBG. Nest box locations were recorded using a global positioning system (GPS) (Garmin GPSmap 60Cx unit) and were downloaded to GPS Utility version 5.02 (2009) to enable plotting on the map of the Botanic Gardens in the GIS software MapInfo version 8.5 (2006). The accuracy of these nest box locations was kept to ≤ 10 and to ≤ 6m where possible.

Figure 2.1 Map of the Cambridge University Botanic Gardens showing the locations of 42 nest boxes. Nest boxes with an 'A' following the number relate to nest boxes erected prior to 2006 with a hole size allowing both blue and great tits to enter. Nest boxes with a 'B' following the number relate to nest boxes erected from 2006 onwards with a hole size allowing only blue tits to enter. The exceptions to this are boxes 8B and 12B, which have a larger hole allowing use by both species. Map courtesy of Getmapping Plc ©.

2.1.2 Population data

For data relating to numbers and ages of blue tits and great tits colour ringed in the CUBG and the associated numbers of individuals found foraging and breeding in nest boxes during the breeding seasons of 2006-2008 please refer to Tables 1-3 (for blue tits) and Tables 4-6 (for great tits) of the Appendix.

CHAPTER 3

Foraging preferences and habitat utilisation by blue tits and great tits in the Cambridge University Botanic Garden during the breeding season

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3.1 Introduction

During the breeding season insectivorous birds such as blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) rely on high protein, high water content lepidopteran larvae to feed their chicks (Gosler 1993; Perrins 1979). The abundance and availability of these larvae affects the quality of the young, as demonstrated by variables such as chick growth and fledging success (e.g. Mägi *et al*. 2009). Choosing where to forage is therefore very important and it has been argued that birds attempt to maximise their foraging efficiency by foraging on invertebrate rich trees (Hino *et al*. 2002). They found, in their study in a Japanese forest, that great tits and willow tits (*Poecile montanus*) preferred tree species with the highest total biomass of invertebrate prey. Other studies have shown that particular bird species usually have particular preferences for the species of tree that they choose to forage on and again this is due to the invertebrate prey found on the individual tree species (e.g. Holmes and Robinson 1981; Peck 1989; Gabbe *et al*. 2002; Park 2005).

Optimal foraging theories (reviews in Pyke *et al*. 1977; Pyke 1984 and Krebs and Kacelnik 1991) would suggest that by having these preferences and choosing specific trees during the breeding season, birds are attempting to maximise their reproductive success by selecting high quality prey (from the chosen trees) for their offspring. This assumes that a forager has some insight into what represents ‘quality’ food for their

offspring and its availability (Houston *et al*. 1980; Sauter *et al.* 2006). Most of these studies examining foraging preferences have been conducted in forest or woodland habitats. However, in today's world, much of the habitat available to birds is in urban areas, usually in the form of parks and gardens (Bland *et al*. 2004; Cannon *et al*. 2005; Hinsley *et al*. 2009) which are usually extremely patchy and heterogeneous. Do breeding birds still attempt to optimise their foraging in these types of habitats by selecting specific vegetation types or species?

Urbanisation has been described as causing loss and degradation of bird habitat and often involves the introduction of exotic plant species (Chace and Walsh 2006) and avian ecologists are becoming increasingly concerned about how the urbanisation of the world is effecting and influencing the structure and compositions of bird communities (Bowman and Marzluff 2001; Chace and Walsh 2006). The planting of exotics may not be a problem for certain (synanthropic) birds such as pigeons and corvids, which appear to benefit from human altered urban habitats (Jokimäki *et al.* 1996). However, the reduction and fragmentation of native vegetation, which urbanisation causes, can be detrimental to many other birds which rely on native species (Donnelly and Marzluff 2006). Various studies of urban birds have also noted that the species most likely to disappear as urbanisation increases are small arboreal insectivores and those likely to do well are omnivorous (e.g. Beissinger and Osborne 1982; Clergeau *et al*. 1998; Crooks *et al* 2004).

Why is exotic vegetation poorer than native vegetation? A study by Southwood *et al.* (1982) found that phytophagous (plant eating) insects have a much lower diversity on introduced trees than native ones. As mentioned previously, many birds such as blue tits and great tits rely on caterpillars, which are phytophages, during the breeding season, and their foraging success could be limited in these types of habitats. Therefore

urbanisation is likely to directly affect arthropod numbers, which are the primary food source for many breeding birds, if exotics are dominant (Bowman and Marzluff 2001).

Also, birds often use environmental clues from plants, such as early leafing, to select their breeding habitat. These environmental clues are usually indicators of fluctuations in food abundance and therefore indicators of when to begin breeding in a particular year (Nilsson and Kallander 2006). In this Swedish study, blue tits and great tits were shown to lay earlier with an early budburst of two native tree species namely silver birch (*Betula pendula*) and English oak (*Quercus robur*). However, early leafing of invertebrate poor exotics may not be a reliable indicator about invertebrate prey availability yet birds may mistakenly use these as such (Remeš 2003). In his study on blackcaps (*Sylvia atricapilla*), Remeš (2003) argues that habitats in an environment that has been much altered by human activity can function as 'ecological traps' by luring birds into unsuitable and inferior breeding habitats. He suggests that breeding productivity of bird populations could be increased by replacing exotic plant species with native ones. Again this poses the question, can breeding birds optimise their foraging in environments with exotic vegetation if they are 'misled' by certain environmental cues?

Martin (1987) discusses parental effort in foraging for food, describing how parent birds face a trade off between their energy reserves and the energy required for the offspring. They (parent birds) should provide sufficient energy to optimise the number of young produced and that go on to survive, both within a breeding season and throughout the parents lifetime (Dhondt 1989). These strategies often mean the offspring receive less than the maximum they could use because the parents need energy for current and future survival to optimise their lifetime reproductive success. In urban parkland however, breeding great tits have been shown to work much harder than in woodland, in

fact 64% harder per chick in terms of daily energy expenditure (Hinsley *et al*. 2008). Hinsley *et al.* (2008) argue that great tits may lack a foraging strategy in selecting their prey therefore resulting in much higher energy costs than blue tits in the same parkland. The artificial environment of urban parkland therefore appears to be making it difficult for great tits to forage optimally.

Blue tits and great tits are insectivorous, arboreal, generalist passerines, which feed their chicks mainly on tree-dwelling caterpillars (Perrins 1979, 1991) and so are good subjects for examining vegetation preferences. From the wealth of studies conducted on these birds it is has been universally accepted that mature oak woodland is their optimal habitat type because oaks offer an abundance of caterpillar prey for foraging parents throughout the breeding season (Kluijver 1951; Lack 1955, 1958; Perrins 1965, 1979, 1991). Nevertheless, this literature has mainly been conducted in woodland environments and literature describing foraging preferences of blue tits and great tits in urban environments is sparse (Cowie and Hinsley 1988). I conducted a study to see how breeding blue tits and great tits were foraging in the available flora in the Cambridge University Botanic Gardens (CUBG). My aim was to discover whether blue tits and great tits foraged in this large urban garden randomly or whether they had specific foraging preferences. To test this the following questions were addressed: 1) Do blue tits and great tits forage preferentially in native over exotic plants in the CUBG? 2) Do they have a leaf-type preference (deciduous or evergreen)? 3) Do they have a plant-type preference (tree or shrub or herbaceous layer? 4) Are key plant genera such as oaks selected preferentially by foraging tits (only blue tits were tested for this question)?

3.2 Methods

3.2.1 Study site

The study was conducted in the CUBG (see Chapter 2 for site description), in which tree and shrub diversity is high with a dominance of exotic flora. Habitat use by foraging blue tits and great tits was measured in the context of the habitat available to them to examine whether their foraging events were randomly distributed across the garden flora.

3.2.2 Collection of habitat data

The available habitat within the CUBG was surveyed using aerial photographs and ground survey. A grid, split into 5m by 5m squares, was created using Grid Maker within the Tool Manager option of the GIS software package MapInfo Professional 8.5 (MapInfo Corporation 2006a), and this was laid over an aerial photograph of the CUBG (Getmapping Plc ©). A total of 22,500 squares (150 by 150 squares) in the grid were labelled consecutively starting with 1 at the bottom left of the grid and ending with 22,500 at the top right of the grid. This ensured coverage of the CUBG and its surrounding areas. The grid was converted in MapBasic 8.5 (MapInfo Corporation 2006b) to a KML file to enable viewing in Google Earth 5.0 (Google Inc 2009). Google Earth had a more up-to-date aerial image of the CUBG in which the vegetation coincided with the bird breeding season (the MapInfo image was taken in late winter).

Sections of the Google Earth aerial images were subsequently printed in colour and used in the field to navigate around the vegetation within the garden. Within each 5m by 5m square, presence or absence data were recorded for the herbaceous layer, shrub

layer, tree canopy, planted bed and maintained hedges. For shrub and tree canopy layers, the following categories were recorded:

i. Genus
ii. Leaf type – evergreen (a plant having green leaves throughout the entire year), deciduous (a plant that sheds its leaves annually) semi-evergreen (a plant that retains green, un-withered leaves for part of the winter or through comparatively mild winters) or 'other' (anything else not categorised)
iii. Origin of plant – native and/or northern/central Europe, Mediterranean and southern Europe, Asia, Americas and 'other' (any other origin not categorised). Most of the flora within the garden was labelled with the species and origin and therefore didn't involve any identification. Garden staff aided in identifying any unlabelled plants. A large part of the flora within the garden was categorised as 'garden variety' in origin meaning a cultivated plant 'whose origin or selection is primarily due to intentional human activity' (Wikipedia 2009). So as to avoid having 'garden variety' as a category of origin and consequently an over-representation of 'garden variety' in the analyses, plants were classed according to where the mother species originated. This included hybrid species where the origin of both parent plants was the same according to my categories. If this was not possible the plant was categorised as 'other'.

A shrub was defined as a woody plant below 5m in height and a tree was defined as a woody plant of 5m and above. The herbaceous layer was defined as any ground-covering native plants such as cow parsley (*Anthriscus sylvestris*) or ivy (*Hedera helix*) but not mown grass. 'Planted beds' were scored when there were obvious planted flower beds containing low lying plants. Any significant woody shrubs that covered the

majority of a 5m square within the bed were recorded as shrubs. A maintained hedge was any vegetation barrier that had been trimmed and kept neat.

If vegetation took up approximately a third or more of the square then it was recorded as available habitat in that particular square. However, if for example, the vegetation spanned across two squares but was only equivalent to one square in size then it was only recorded as available in one of the squares selected randomly. Approximately 80% (4585 squares) of the garden was mapped, excluding the lake and garden at the Bateman Street entry end where relatively few foraging observations of blue tits had been made.

3.2.3 Foraging observations

Two separate analyses were carried out to test blue tit and great tit foraging preferences (see Chapter 5, methods, for a description of foraging observations). One analysis tested both blue tits and great tits by using a single random observation of each individual, with a sample size reflecting the total number of known individuals observed foraging in the CUBG (described below in section *3.2.3.1*). The second analysis was carried out on a smaller number of blue tits, which had been part of a more intensive investigation during the 2008 breeding season. This was so as much information as possible on individuals could be collected as the particular analysis (compositional analysis) that was to be used enabled multiple observations of an individual to be tested without the usual problems associated with repeated measures (see section *3.2.4.1* below for a more detailed explanation of compositional analysis). In the previous two breeding seasons, despite a vast number of overall observations having been collected, only a small number of foraging observations per individual had been obtained. Therefore in order to maximise the number of observations of each individual a tighter focus on a smaller number of blue tits was required. To further maximise individual observations,

observations from a bird from previous years were used if the same individual had used the same nest box.

3.2.3.1 Blue tit and great tit foraging observations

To analyse the habitat use of both blue tits and great tits throughout all breeding seasons (2006-2008) only one observation of an individual was used. This was to prevent pseudoreplication with repeated observations of the same individual. The observation was selected by using random number calculation in Microsoft Office Excel version 10 (Microsoft Corporation 1985-2001). The data were then sorted by species and then by individual (by their colour ring) and then the first observation from the lowest random number was selected for the analyses. Separate random number categories were generated to answer different questions; data were sorted in Excel by species, then plant use (tree or shrub) and then by individual. Each observation of an individual from the lowest random number in each plant type category (tree or shrub) was then selected. In this way, the probability of a bird feeding on trees of different origins could be analysed, using data for observations of individuals feeding on trees only (not shrubs).

The protocols outlined above were carried out on the entire data set, and then repeated for three separate periods within the breeding season, from egg laying to the fledgling stage. Data were sorted into period one (nest building, egg laying and incubation) period two (chick feeding) and period three (fledging - when the adults were seen with their young foraging outside of the box). Again, within each of these periods, the lowest random number of an observation of an individual was selected (so an individual may have appeared separately in all three breeding periods). The dates of the different breeding periods were selected by averaging nest box data within years. Period one was defined by the date of the first observations made in a year (usually the beginning of

April) until the day before the average hatching date of that year. Period two was from the average hatching date until the average date at which the chicks were 17 days of age. Period three was from the average date at which the chicks were 18 days of age until the observations were stopped (usually late June). Blue tit and great tit chicks generally fledge at 18 days of age, which is why this date was chosen as the average of fledging. The data was checked to confirm that within each year the first observation of a fledgling blue tit and great tit did not differ wildly from the average date calculated from the nest box data of chicks at 18 days of age.

The breeding period data was further sorted into plant use (tree or shrub) (as described above for data throughout the whole breeding season). A final category sorted the data into species and then breeding season, splitting the years 2006, 2007 and 2008. Once more, within each of these years, the lowest random number of an observation of an individual was selected.

3.2.4 Statistical analyses

3.2.4.1 Compositional analysis

Compositional analysis (Aitchison 1986; Aebischer *et al.* 1993) using the Compos Analysis v6.2+ software Excel Add-In tool (Smith 2005) was carried out to evaluate whether blue tits were using a particular habitat type significantly more than random. This method uses Multivariate Analysis of Variance (MANOVA) (Wilks' lambda Λ) to analyse compositional data i.e. where the variables are represented as proportions (or percentages) and sum to a whole. The principle of the method is to transform the compositional data into log ratios and then use MANOVA to test the statistical significance between the variables. Then, the order of these differences is ranked to

reveal which habitat type(s) (variable) may be utilised more than any other(s). Compositional analysis was used for a number of reasons. Firstly, as repeated observations of the same individual are usually not independent, because an animal's activity at one time is often influenced by its behaviour at a previous time, an analysis was needed that could optimise multiple individual observations without inflating the degrees of freedom by pooling data across animals (Aebischer *et al*. 1993). Compositional analysis avoids this problem by using individuals as sampling units with the sample size being the number of colour ringed birds rather than the number of observations. Secondly, it is unaffected by the unit-sum constraint, where the proportions describing use or availability of habitat sum to one and therefore mean that the proportions are not independent of each other (Aitchison 1986). This is because greater proportional use of one habitat type implies less use of another and to treat them as independent would be incorrect (Aebischer and Robertson 1994). Thirdly, compositional analysis also allows definition of available habitat to be catered to an individual bird (100m around a nest box) rather than defining habitat for the total study area (the whole of the CUBG). The whole area of a study site would not be available to an individual due to the presence of conspecifics and due to the constraints (in terms of distances travelled) of chick feeding.

The habitat available to a particular blue tit was calculated in MapInfo by creating a 100m radius buffer around its nest box (nest box points were recorded using a GPS unit then imported into MapInfo and layered over the aerial photo and grid) and all grid squares within that buffer were selected and exported as a CSV file. 11 blue tit nest boxes in total were used in these analyses.

The habitat within each 100m buffer was then categorised and percentages calculated within each category to enable multiple compositional analyses. Since the habitat

available to a bird in one square could be in several levels on a 3D scale (e.g. tree canopy, shrub layer and herbaceous layer), each category within a square was counted as '1'. So for example, if an area was completely covered with tree canopy and shrubbery, the total habitat available would be 2x an area covered with just shrub and would be given a count of '2'.

Due to the relative infrequency of maintained hedges, and because they spanned little of a 5m square, they, along with planted beds in which blue tits were not observed foraging, and any squares not falling into any of the other categories, were grouped as 'un-utilisable habitat/gap' and given a count of '1'. If a square also contained 'planted bed' and 'maintained hedge' they were only counted as '1' so as not to over-estimate un-utilisable habitat. 'Planted bed' and 'maintained hedge' were only scored in the absence of herbaceous layer/shrub/canopy to identify heterogeneity in open habitat. Thus the percentages were calculated from a total that included the sum of all these 'levels' within a 100m nest box buffer. Any squares within a 100m buffer that were outside the CUBG or that were inaccessible areas within the CUBG (e.g. the caretaker's house) were excluded from the total count. Also excluded from the analyses was any unidentified vegetation, which amounted to an average of 0.22% of the trees and 0.62% of the shrubs around the 11 boxes.

The utilised habitat, taken from the observations of individual foraging blue tits, was categorised in the same way as the available habitat and the 'used habitat' and 'available habitat' were then exported into the associated work sheets in the compositional analysis program. A sequence of compositional analyses was then carried out, addressing each of the research questions. Cases were weighted by the square root of the number of foraging observations of individual birds to adjust for any differences in the quantity of data collected for each bird. Each analysis accepted the program default

of 1000 iterations and any zero values in the used habitat, corresponding to a non-utilised but available habitat were replaced by the appropriate value calculated by the program. The program determined this value by reference to the smallest 'available' or 'used' value present, creating a new value that was an order of magnitude smaller than this smallest number (Smith 2005).

Zero values in the used habitat are a problem since log ratios cannot be calculated for them and the usual method to control for this is to substitute the zero with a small positive value (e.g. Aebischer *et al*. 1993). For each of my analyses, this substituted value ranged from 0.1 to 0.001 and is reported in the results of each test. This problem of the zero value has been argued as a weakness in compositional analysis and substituting the zero with an arbitrary value is also not without its problems (Elston *et al*. 1996). The effect of different zero values for example may of course affect the outcome of the test results. The zero values were therefore substituted in turn with 1, 0.1, 0.01, 0.001 and 0.0001 to test for any zero substituting effects on the Wilks' lambda and ranking matrices (as in Aebischer *et al*. 1993).

To avoid the need to drop any whole variables (e.g. habitat categories or bird foraging observations), any 'available' values that were zero, meaning a particular habitat type around a particular box was not available for use by an individual at that box, were treated as missing values by the program, as recommended by Aebischer *et al.* (1993) (in Appendix 2, option 3). In this method, log ratio means from non-missing available habitat(s) are used to calculate the log ratio for the missing (or zero valued) available habitat. Once run, the program ranks the habitat categories in order of use and determines any associated significance values between these categories by t-values.

A total of 10 compositional analyses testing 22 individual birds at 11 nest box sites were performed to examine blue tit foraging preferences in the CUBG. Due to the relatively small number of observations of each individual, foraging data from nest building/egg laying/incubation and chick feeding were pooled. Foraging observations from adults with fledglings were not included since the adults were now not necessarily confined to just the habitat around the nest box and could move about the CUBG and surrounding areas; thus the habitat available could not be accurately calculated.

The first two tests examined blue tit foraging in the different plant origins and leaf types (evergreen or deciduous) within the CUBG. The third test examined blue tit foraging in the different plant types (tree, shrub and herbaceous layers) within the CUBG. For all tests, the word 'native' indicates plant species native to Britain and northern and central Europe. The habitat categories for the first three tests are outlined below:

1. a) native trees and shrubs b) Asian trees and shrubs c) Americas trees and shrubs d) Mediterranean/south European trees and shrubs e) Other trees and shrubs f) herbaceous layers g) un-utilisable habitat or gap

2. a) native deciduous trees and shrubs b) non-native deciduous trees and shrubs c) native evergreen trees and shrubs d) herbaceous layers e) non-native evergreen trees and shrubs f) un-utilisable habitat or gap

3. a) deciduous trees b) deciduous shrubs c) evergreen trees d) herbaceous layers e) evergreen shrubs f) un-utilisable habitat or gap

Subsequent analyses examined use of genera. In one analysis, the top seven utilised genera by blue tits in the CUBG, namely *Acer, Betula, Fagus, Populus, Prunus*,

Quercus and *Sorbus* were tested against each other, disregarding origin, and against all other deciduous trees and shrubs omitting the seven genera and all other evergreen trees and shrubs omitting the seven genera (if the chosen genera had any evergreen species). The herbaceous layer and un-utilisable habitat/gap categories were also tested in the analysis.

To test for origin preferences within each genus all genera (excluding *Fagus* because all *Fagus* within the garden was native) were split into native and non-native categories. Each genus category (native/non-native) was then tested against each other and against all deciduous trees and shrubs together omitting the chosen genus, all evergreen trees and shrubs together omitting the chosen genus (if the chosen genus had any evergreen species) and the herbaceous layer and the un-utilisable habitat/gap categories.

The tests were first ran including the un-utilisable habitat/gap category but as blue tits never used this category, consequently it was always ranked significantly as the lowest, which may have biased the P value inaccurately. Therefore, this category was removed from the analysis and the tests re-ran. Although this meant that the available habitat did not now equal 100%, because the 'used' un-utilisable habitat/gap category was always zero this meant that MANOVA tests between the calculated log ratios of the remaining habitat categories would be unaffected and the test would still be valid (Aebischer *et al* 1993; Smith 2005).

3.2.4.2 Frequency tests

Frequency tests were carried out using all foraging observations from 2006-2008 of both blue tits and great tits. One observation of each individual of each species was chosen using the random number selection outlined above (section *3.2.3.1*) to test used

habitat against the available habitat. These tests examined foraging both across the seasons and within the seasons by splitting it down into three breeding periods. In SPSS 13.0 for Windows (SPSS Inc 2004) two-way G tests using the asymptotic significance value were used to test for any variation in blue tit and great tit foraging between years and to see if it would be correct to pool the data (if little variation existed).

Chi-square goodness-of-fit tests using the Monte Carlo significance value were used to analyse blue tit and great tit foraging use in the CUBG. The Monte Carlo method calculates a more accurate significance level than the default asymptotic calculation without relying on assumptions that might not have been met when accepting or rejecting the null hypothesis. For example, results from small data sets or results from tests where the expected frequencies are less than 5 may not be trustworthy (Hawkins 2005). All of the vegetation within the sampled area of the CUBG was categorised in the same way as in the 100m buffers (see above, section *3.2.4.1*) and the percentages of available habitat were calculated to give results for the whole garden as opposed to individual boxes. These percentages were then entered as expected values in the chi-square tests. This allowed all the remaining observations that weren't used in the compositional analyses, including great tits, to be analysed. Although not as powerful a test as the compositional analyses, the chi square tests could be used to see if the blue tit results supported the compositional analyses results and also whether great tits differed from blue tits in their habitat use.

Blue tits and great tits were tested separately for their foraging use in: a) trees and shrubs of different origins b) trees of different origins c) shrubs of different origins d) different plant types e) different leaf types. The same tests were then repeated separately for each breeding period.

To improve the reliability of each test, since the chosen observation of a specific individual may not have been representative of its usual behaviour, the tests were repeated six times using different observations chosen by six different random numbers. The number of significant tests out of the six were tabulated. Test values and significance levels were only reported for two of the tests, those having the highest P value (or lowest chi-square/G-test value) and those having the lowest P value (or highest chi-square/G-test value). In many cases the number of individuals (N) reported in these two tests differ slightly and this is as a result of the random number selection including some birds that had been foraging in the un-surveyed area of the CUBG. These individuals were omitted from the tests in SPSS, which resulted in a slight lowering of N. Birds found in 'herbaceous layers' were also omitted for all tests except those looking at blue tit and great tit use of plant type, which again may have affected N slightly.

3.3 Results

3.3.1 Blue tit foraging preferences around nest boxes

Table 3.1 shows the total number of observations made of individual blue tits that were used in the compositional analyses. There was a slight bias towards total male observations (189) compared to total female observations (159), which probably reflects time the females spent incubating. The multivariate Wilk's lambda test in the analyses shows that blue tit foraging differed significantly from random at the $P \leq 0.05$ in two cases and $P \leq 0.005$ in eight of the cases (Table 3.2).

Simplified ranking matrix tables generated by each test ranked the blue tits according to their foraging use in the various habitat types (Tables 3.3 – 3.12). Along with each of

these tables, Figures 3.1 to 3.10 show how the habitats as defined in each of the tests, were used by the foraging blue tits relative to the habitats' availability by taking an average of the 'used' and 'available' values. Table 3.3 and Figure 3.1 shows blue tits having significantly greater foraging use in native and northern/central European trees and shrubs than in Asian, American, Mediterranean/southern European and 'other' trees and shrubs. These latter four categories, although ranked in order of preference, did not differ significantly in their foraging use by blue tits so their ranking meant little. Asian, American and Mediterranean/southern European trees and shrubs were used significantly more than the herbaceous layer, which was the least used.

Since the latter four categories did not differ in their use, they were pooled as a non-native category and then split into evergreen and deciduous categories (Table 3.4 and Figure 3.2). Native deciduous trees and shrubs were used significantly more by blue tits than all other categories in this test. Both native and non-native deciduous trees and shrubs were used significantly more than native and non-native evergreen trees and shrubs, which, along with herbaceous layers, didn't differ significantly in their use.

A third analysis tested for differences in foraging use in trees and in shrubs and showed that deciduous trees were preferred foraging habitat, being ranked significantly higher than all other categories (Table 3.5). This difference is also demonstrated in Figure 3.3, where the use of deciduous trees is much greater than their availability. As before, all deciduous categories were significantly preferred over all evergreen categories and although evergreen trees were ranked above evergreen shrubs this preference was not significant.

Blue tits were found foraging in *Betula* trees and shrubs significantly more than any of the other focal tree and shrub genera (*Acer, Populus, Quercus, Prunus, Sorbus and*

Fagus) (Table 3.6). *Fagus* trees and shrubs, being ranked 9th, showed a tendency to be avoided by blue tits. Apart from *Betula*, only *Acer* trees and shrubs (among the 'focal' taxa) were significantly preferred over *Fagus*. Figure 3.4 shows that all focal genera were used to a greater extent than their availability and that the extent of this difference mostly coincided with the ranked order of preference, i.e. the difference between the used and available values of the most preferred genera *Betula* was much greater than the difference between the used and available values of the least preferred genera, *Fagus.* Nevertheless, from Figure 3.4 *Quercus* appears to be being used, relative to its availability, to a much greater extent than its placement in the ranking order would suggest, second to *Betula*. There also appeared to be much less of a difference between used and available values of 'all other deciduous trees and shrubs', which was ranked as second. Looking at the error bars however it can be seen that there was a lot of variation across used values, especially for *Quercus* and therefore by averaging the used and available values in this particular case, a figure had been created that is not entirely reflective of the compositional analysis results.

Tests were then carried out to see if native trees and shrubs from the focal genera (apart from *Fagus* as all *Fagus* trees in the CUBG were natives) were used preferentially over non-natives. In all tests (Tables 3.7, 3.8, 3.9, 3.10, 3.11. and 3.12), only native *Betula* was found to be significantly preferred over non-natives in the same genus (Table 3.7); a difference also demonstrated by Figure 3.5 showing their greater use of native *Betula* relative to availability than for non-native *Betula.* However, native *Acer*, *Populus* and *Quercus* trees and shrubs were ranked as second in their tests and this preference may not have been significant over lower ranked categories due to a small number of observations being made in the specific genera. Figures 3.6 (for *Acer*) and Figure 3.7 (for *Quercus*) do suggest a greater use of the native genera over the non-native genera (relative to availability) supporting this, although this was not so in *Populus* (Figure

3.8). There was also relatively little difference in use relative to availability in native and non-native *Sorbus* (Figure 3.9) and native and non-native deciduous *Prunus* (Figure 3.10) supporting the findings from the compositional analyses for these genera (Table 3.10 for *Prunus* and Table 3.12 for *Sorbus*).

Therefore it can be seen that the key foraging habitats in the breeding period for blue tits appear to be deciduous trees, with deciduous shrubs being secondary and with *Betula* being the preferred genus. Evergreen trees and shrubs tended to be avoided as did, to a lesser extent, herbaceous layers and *Fagus* trees and shrubs.

3.3.1.1 Effect of substituting zero with differing small values

In the above examples an unutilised but available habitat category was assigned a small positive value by the compositional program; depending on the lowest 'available' or 'used' value the program assigned a value an order of magnitude lower than this (rather than 0). Tables 3.13 and 3.14 show the effect of using different values as a substitute for zero compared with the program default. In all cases but one the value replacing zero still generated a significant result in the Wilk's lambda test (randomisation $P \leq 0.05$ and ≤ 0.005 in most cases) meaning that blue tits were still foraging non-randomly. The one case that did not have a significant result was where the value replacing zero was 0.01 (relatively high) in the test comparing the different genera (Table 3.14d). All P values were higher in all the substituted zero tests comparing genera than in all other tests and this may have been because of the greater number of habitat categories (10) being compared.

From Table 3.13 it can be seen that in all of the tests for replacement values between 0.1 to 0.0001% the results seem quite robust. All replacement values still maintained the

number one rank as the most preferred habitat and maintained its significance level over the 2nd placed habitat and the other habitats were still ranked similarly, with the same significance level between preceding ranks. Habitats that did change places in their ranking order were ones which did not differ significantly from each other in their use and usually ranks only swapped with the previous or subsequent rank. At the 1% level however, the rankings seem to change more markedly with for example in 3.13a habitat E ('other' trees and shrubs) moved from being ranked 5th in the default test to being ranked 2nd at the 1% level. If you replace a zero with a number that is close to the lowest value in the 'used' or 'available' habitats you will start to affect the results inaccurately by over-estimating use in certain habitats. Take the example in 3.13a, the 'available' values in habitat E ranged from 5.03% to 1.42%. By substituting a zero value in the 'used' habitat E with 1%, a blue tit appears to be using habitat E more or less as expected by chance rather than underutilising it as indicated by the true zero value. Thus habitat E has been over-estimated in its use and has therefore moved up the ranks from 5th to 2nd.

Table 3.13a-c had default replacement values of 0.1% (selected by the program). However, with Table 3.14, in all tests except 3.14b the default substituted zero value was 0.001% meaning that the lowest 'available' or 'utilised' value was between 0.01 - 0.09. From these tests it can be seen that generally the lower substituted values (0.0001 – 0.01%) generate similar results with only the lower ranked non-significant habitats swapping places. However, if the substitute value increases to 0.1 and 1% the rankings change even more markedly than the tests with the default replacement value of 0.1% (Table 3.14a-c). So, for example, in the case of 3.14d, habitat A (all deciduous trees and shrubs minus deciduous *Prunus*) drops its significance over habitat B (all non-native deciduous *Prunus* trees) at the 0.1% level and drops down to being ranked 3rd at the 1% level with category D (all native *Prunus* trees and shrubs) being ranked significantly

higher in 2nd place. Again this is as a result of many of the 'available' values being very low (e.g. between 0.06% – 4.15% in table 3.14d, *Prunus* habitats B, D and F) and means that the tests using a default value 100 or 1000 times greater than the default replacement value are overestimating blue tit foraging use in these habitats and inaccurately ranking them higher.

To replace the zero values with a value an order of magnitude lower than the lowest 'available' or 'used' value as carried out by the program and suggested by Aebischer *et al* (1993) therefore appears to be the most appropriate and accurate test to perform.

Table 3.1 Number of observations taken for each individual blue tit that was used in the compositional analysis tests. The tests were weighted by the square root of these observations.

Box number	Colour ring	Male (M) or female (F)	Years included in the data	Number of observations
1b	P/G-B	M	2008	18
1b	Y/G-R	F	2008	9
2b	R+G	M	2008	21
2b	R-W/Y	F	2008	7
3b	Y/W-R	M	2008	12
3b	W/B	F	2006, 2007, 2008	21
4b	Y+B	M	2008	21
4b	R-W/R	F	2008	6
5b	G-O/B	M	2008	14
5b	W+B	F	2008	8
7b	R-B/G	M	2007, 2008	18
7b	W/G-O	F	2006, 2007, 2008	19
9b	W/G-R	M	2008	12
9b	B+P	F	2008	6
10b	P/R-B	M	2006, 2008	31
10b	R-B/O	F	2007, 2008	50
11b	G/R-B	M	2007, 2008	11
11b	O/W-M	F	2007, 2008	11
18b	R+B	M	2008	13
18b	R-B/Y	F	2008	15
21b	P+W	M	2008	18
21b	W/Y-B	F	2008	7

Table 3.2 Compositional analysis test results showing the Wilk's lambda value and its associated significance level and degrees of freedom. See individual simplified ranking matrix tables (3.3-3.12) for the habitat categories that each test compares.

Test	Simplified ranking matrix table number	Wilks Lambda	*df*	Randomisation *P*
All origins	3.3	0.298	5	0.002
Deciduous vs evergreen origins	3.4	0.160	4	0.001
Tree vs shrub	3.5	0.111	4	0.001
Focal genera	3.6	0.271	9	0.046
Acer	3.7	0.202	4	0.001
Betula	3.8	0.219	4	0.001
Populus	3.9	0.178	4	0.013
Prunus	3.10	0.168	5	0.001
Quercus	3.11	0.200	5	0.005
Sorbus	3.12	0.089	4	0.001

Table 3.3 Simplified ranking matrix from compositional analysis for blue tits based on their foraging use of the different tree and shrub origins available in the CUBG around an individual's nest box. For this test evergreen and deciduous plants have been combined. Triple signs (+++) indicate a significant preference at $P < 0.05$ for foraging habitats down the left hand column relative to those along the top row and single signs (+) indicate a non-significant preference. Ranks indicate the most preferred (1) and most avoided (6) habitats.

	B	C	D	E	F	Rank
Native trees and shrubs (A)	+++	+++	+++	+++	+++	1
Asia trees and shrubs (B)		+	+	+	+++	2
Americas trees and shrubs (C)			+	+	+++	3
Med/south Europe trees and shrubs (D)				+	+++ (+)	4
Other trees and shrubs (E)					+	5
Herb layer (F)						6

[1] Significance levels and ranks are shown according to randomization results, but where significance levels from standard t-tests of observed data differ these are shown in parentheses.

[2] "Used' values of 0% where corresponding 'Avail' was nonzero were replaced by 0.1

Table 3.4 Simplified ranking matrix from compositional analysis for blue tits based on their foraging use of the different tree and shrub origins available in the CUBG around an individual's nest box where all non-native origins (Americas, Asia, Med/south Europe and 'Other') have been combined. For this test evergreen and deciduous plants have been separated. Triple signs (+++) indicate a significant preference at $P < 0.05$ for foraging habitats down the left hand column relative to those along the top row and single signs (+) indicate a non-significant preference. Ranks indicate the most preferred (1) and most avoided (5) habitats.

	B	C	D	E	Rank
Native deciduous tree and shrub (A)	+++	+++	+++	+++	1
Non-native deciduous tree and shrub (B)		+++	+++	+++	2
Native evergreen tree and shrub (C)			+	+	3
Herb layer (D)				+	4
Non-native evergreen tree and shrub (E)					5

[1] 'Used' values of 0% where corresponding 'Avail' was nonzero were replaced by 0.1

Table 3.5 Simplified ranking matrix from compositional analysis for blue tits based on their foraging use of the evergreen or deciduous trees or evergreen or deciduous shrubs available in the CUBG around an individual's nest box. Triple signs (+++) indicate a significant preference at $P < 0.05$ for foraging habitats down the left hand column relative to those along the top row and single signs (+) indicate a non-significant preference. Ranks indicate the most preferred (1) and most avoided (5) habitat types.

	B	C	D	E	Rank
Deciduous tree (A)	+++	+++	+++	+++	1
Deciduous shrub (B)		+++	+++	+++	2
Evergreen tree (C)			+	+	3
Herb layer (D)				+	4
Evergreen shrub (E)					5

[1] 'Used' values of 0% where corresponding 'Avail' was nonzero were replaced by 0.1.

Table 3.6 Simplified ranking matrix from compositional analysis for blue tits based on their foraging use of focal tree and shrub genera available in the CUBG around an individual's nest box. For this test evergreen and deciduous *Quercus* and evergreen and deciduous *Prunus* plants have been combined respectively. All other plant genera were represented only by deciduous plants. Triple signs (+++) indicate a significant preference at $P < 0.05$ for foraging habitats down the left hand column relative to those along the top row and single signs (+) indicate a non-significant preference. Ranks indicate the most preferred (1) and most avoided (10) habitat types.

	B	C	D	E	F	G	H	I	J	Rank
All *Betula* trees and shrubs (A)	+	+	+++	+++	+++	+++	+++	+++	+++	1
All other deciduous trees and shrubs (B)		+	+++	+++	+++	+++	+++	+++	+++	2
All *Acer* trees and shrubs (C)			+	+	+	+	+	+++	+++	3
All *Populus* trees and shrubs (D)				+	+	+	+	+	+	4
All *Quercus* trees and shrubs (E)					+	+	+	+	+	5
All *Prunus* trees and shrubs (F)						+	+	+	+	6
All *Sorbus* trees and shrubs (G)							+	+	+	7
Herb layer (H)								+	+	8
All *Fagus* trees and shrubs (I)									+	9
All other evergreen trees and shrubs (J)										10

[1] 'Used' values of 0% where corresponding 'Avail' was nonzero were replaced by 0.001.

Table 3.7 Simplified ranking matrix from compositional analysis for blue tits based on their foraging use of the native and non-native *Betula* trees and shrubs available in the CUBG around an individual's nest box. Triple signs (+++) indicate a significant preference at $P < 0.05$ for foraging habitats down the left hand column relative to those along the top row and single signs (+) indicate a non-significant preference. Ranks indicate the most preferred (1) and most avoided (5) habitat types.

	B	C	D	E	Rank
All native *Betula* trees and shrubs (A)	+	+++	+++	+++	1
All deciduous trees and shrubs minus *Betula* (B)		+++	+++	+++	2
All non-native *Betula* trees and shrubs (C)			+	+	3
Herb layer (D)				+	4
All evergreen trees and shrubs (E)					5

[1] 'Used' values of 0% where corresponding 'Avail' was nonzero were replaced by 0.01

Table 3.8 Simplified ranking matrix from compositional analysis for blue tits based on their foraging use of the native and non-native *Acer* trees and shrubs available in the CUBG around an individual's nest box. Triple signs (+++) indicate a significant preference at $P < 0.05$ for foraging habitats down the left hand column relative to those along the top row and single signs (+) indicate a non-significant preference. Ranks indicate the most preferred (1) and most avoided (5) habitat types.

	B	C	D	E	Rank
All deciduous trees and shrubs minus *Acer* (A)	+++	+++	+++	+++	1
All native *Acer* trees and shrubs (B)		+	+	+	2
Herb layer (C)			+	+	3
All non-native *Acer* trees and shrubs (D)				+	4
All evergreen trees and shrubs (E)					5

[1] 'Used' values of 0% where corresponding 'Avail' was nonzero were replaced by 0.001

Table 3.9 Simplified ranking matrix from compositional analysis for blue tits based on their foraging use of the native and non-native *Populus* trees and shrubs available in the CUBG around an individual's nest box. Triple signs (+++) indicate a significant preference at $P < 0.05$ for foraging habitats down the left hand column relative to those along the top row and single signs (+) indicate a non-significant preference. Ranks indicate the most preferred (1) and most avoided (5) habitat types.

	B	C	D	E	Rank
All deciduous trees and shrubs minus *Populus* (A)	+++	+++	+ (+++)	+++	1
All native *Populus* trees and shrubs (B)		+	+	+	2
Herb layer (C)			+	+	3
All non-native *Populus* trees and shrubs (D)				+	4
All evergreen trees and shrubs (E)					5

[1] Significance levels and ranks are shown according to randomization results, but where significance levels from standard t-tests of observed data differ these are shown in parentheses.

[2] "Used' values of 0% where corresponding 'Avail' was nonzero were replaced by 0.001

Table 3.10 Simplified ranking matrix from compositional analysis for blue tits based on their foraging use of the native and non-native and evergreen and deciduous *Prunus* trees and shrubs available in the CUBG around an individual's nest box. Please note that all native *Prunus* trees and shrubs were deciduous. Triple signs (+++) indicate a significant preference at $P < 0.05$ for foraging habitats down the left hand column relative to those along the top row and single signs (+) indicate a non-significant preference. Ranks indicate the most preferred (1) and most avoided (6) habitat types.

	B	C	D	E	F	Rank
All deciduous trees and shrubs minus deciduous *Prunus* (A)	+++	+++	+++	+++	+++	1
All non-native deciduous *Prunus* trees and shrubs (B)		+	+	+	+++	2
Herb layer (C)			+	+	+	3
All native *Prunus* trees and shrubs (D)				+	+	4
All evergreen trees and shrubs minus evergreen *Prunus* (E)					+	5
All non-native evergreen *Prunus* trees and shrubs (F)						6

[1] 'Used' values of 0% where corresponding 'Avail' was nonzero were replaced by 0.001

Table 3.11 Simplified ranking matrix from compositional analysis for blue tits based on their foraging use of the native and non-native and evergreen and deciduous *Quercus* trees and shrubs available in the CUBG around an individual's nest box. Please note that all native *Quercus* trees and shrubs were deciduous. Triple signs (+++) indicate a significant preference at $P < 0.05$ for foraging habitats down the left hand column relative to those along the top row and single signs (+) indicate a non-significant preference. Ranks indicate the most preferred (1) and most avoided (6) habitat types.

	B	C	D	E	F	Rank
All deciduous trees and shrubs minus deciduous *Quercus* (A)	+	+++	+++	+++	+++	1
All native *Quercus* trees and shrubs (B)		+	+	+	+	2
All non-native deciduous *Quercus* trees and shrubs (C)			+	+	+	3
All non-native evergreen *Quercus* trees and shrubs (D)				+	+	4
Herb layer (E)					+	5
All evergreen trees and shrubs minus evergreen *Quercus* (F)						6

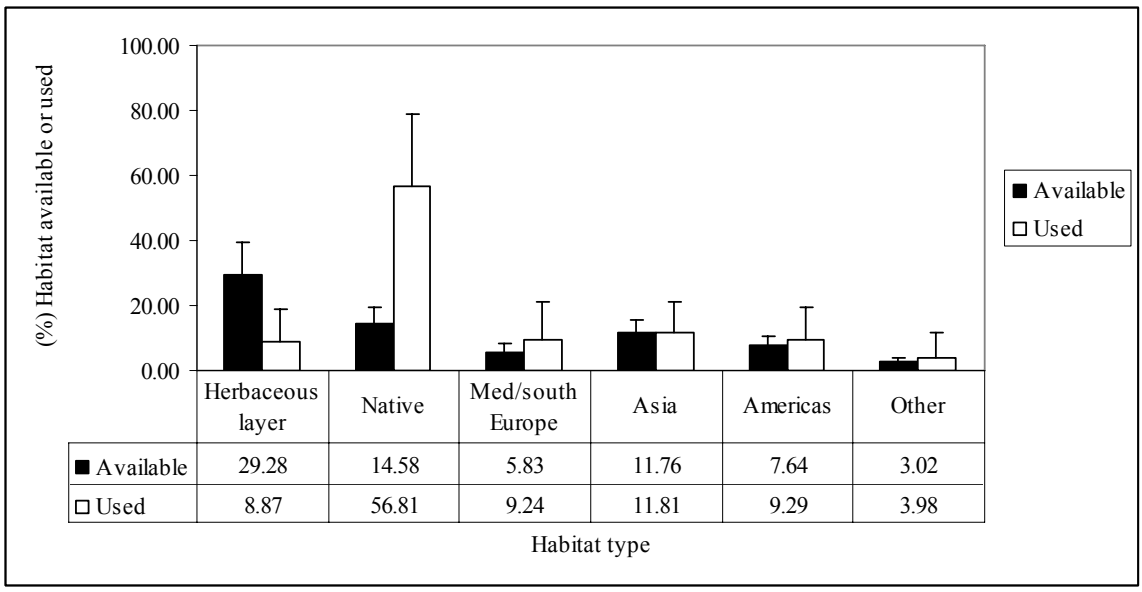
[1] 'Used' values of 0% where corresponding 'Avail' was nonzero were replaced by 0.001

Table 3.12 Simplified ranking matrix from a compositional analysis test for blue tits based on their foraging use of the native and non-native *Sorbus* trees and shrubs available in the CUBG around an individual's nest box. Triple signs (+++) indicate a significant preference at $P < 0.05$ for foraging habitats down the left hand column relative to those along the top row and single signs (+) indicate a non-significant preference. Ranks indicate the most preferred (1) and most avoided (6) habitat types.

	B	C	D	E	Rank
All deciduous trees and shrubs minus *Sorbus* (A)	+++	+++	+++	+++	1
Herb layer (B)		+	+	+	2
All native *Sorbus* trees and shrubs (C)			+	+	3
All evergreen trees and shrubs (D)				+	4
All non-native *Sorbus* trees and shrubs (E)					5

[1] 'Used' values of 0% where corresponding 'Avail' was nonzero were replaced by 0.001

Figure 3.1 Blue tit foraging use relative to availability of the different tree and shrub origins in the CUBG where evergreen and deciduous plants have been combined in the tree and shrub categories. Data have been averaged over all the blue tit nest boxes (n = 11) used in the compositional analyses.



	Herbaceous layer	Native	Med/south Europe	Asia	Americas	Other
Available	29.28	14.58	5.83	11.76	7.64	3.02
Used	8.87	56.81	9.24	11.81	9.29	3.98

Figure 3.2 Blue tit foraging use relative to availability of the different tree and shrub origins in the CUBG where all non-native origins (Americas, Asia, Med/south Europe and 'Other') have been combined and where evergreen and deciduous plants have been separated in the tree and shrub categories. Data have been averaged over all the blue tit nest boxes (n = 11) used in the compositional analyses.

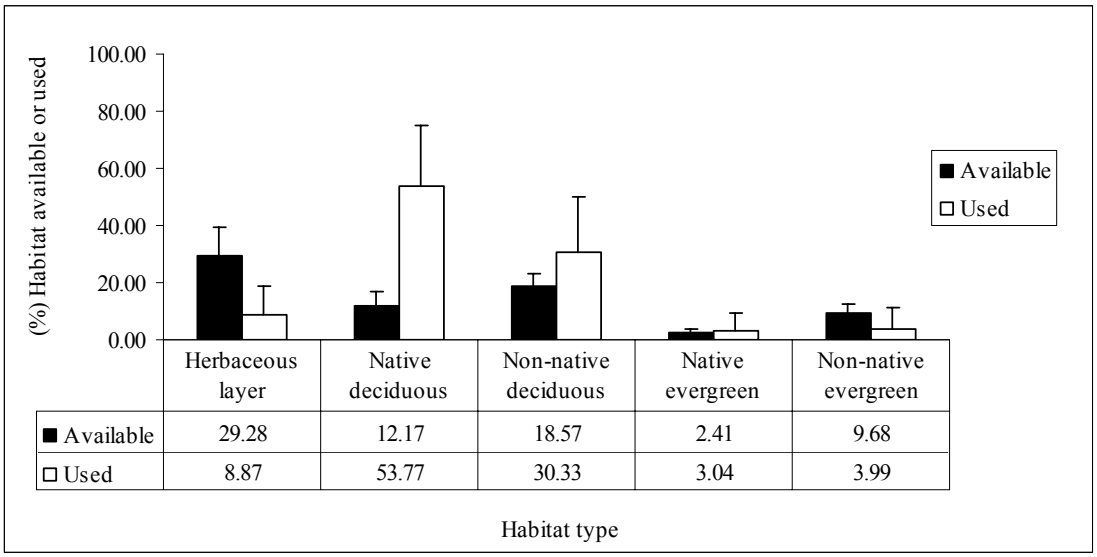
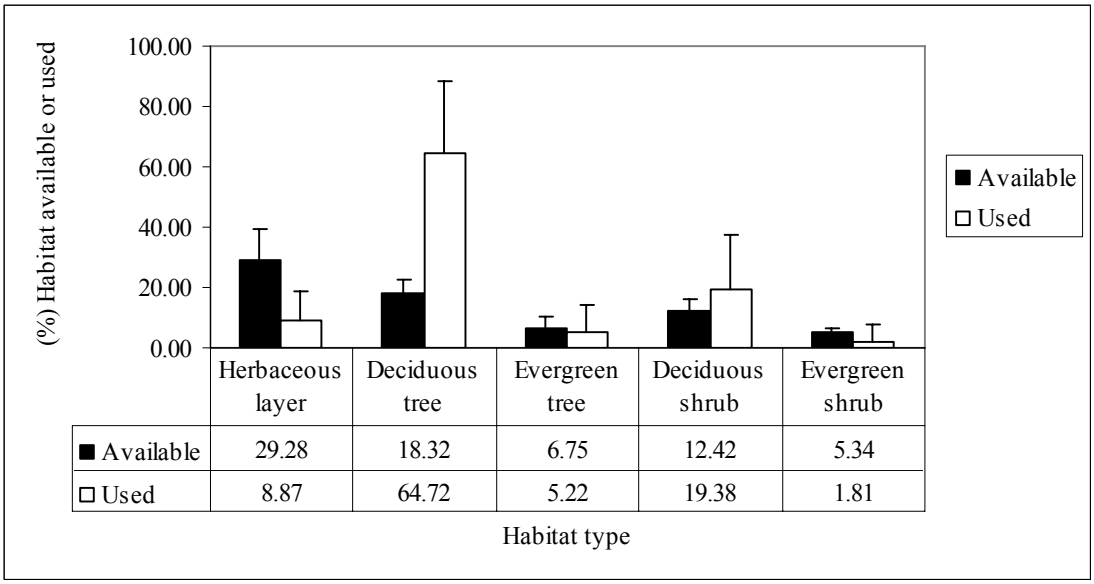
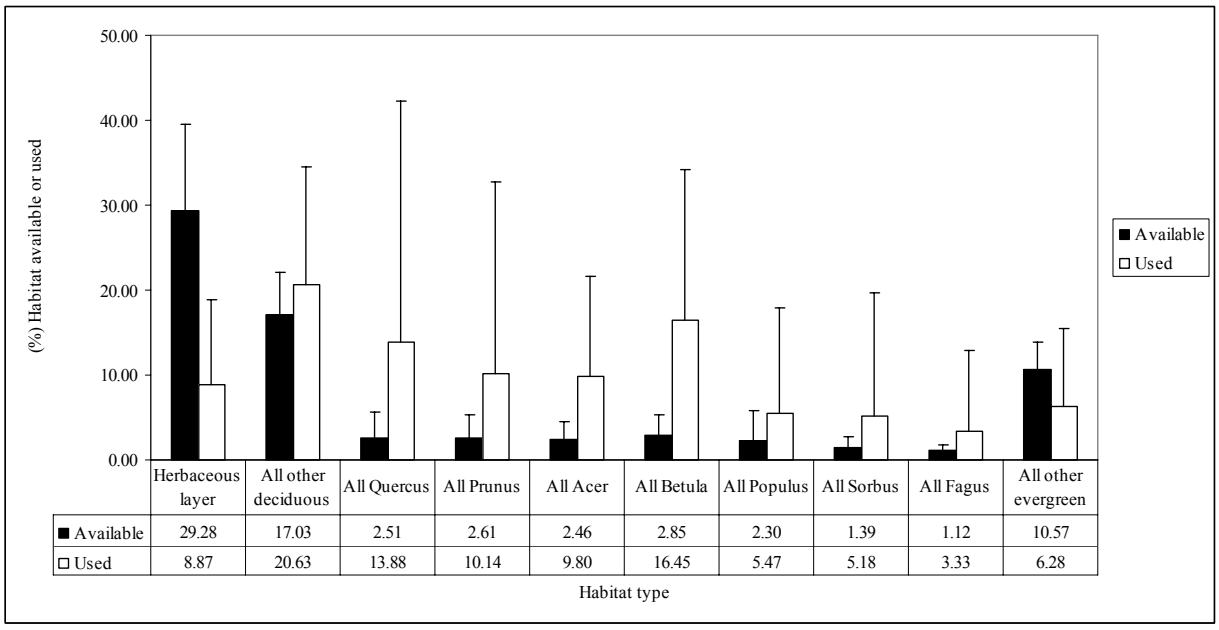


Figure 3.3 Blue tit foraging use relative to availability of the evergreen or deciduous trees or evergreen or deciduous shrubs in the CUBG. Data have been averaged over all the blue tit nest boxes (n = 11) used in the compositional analyses.



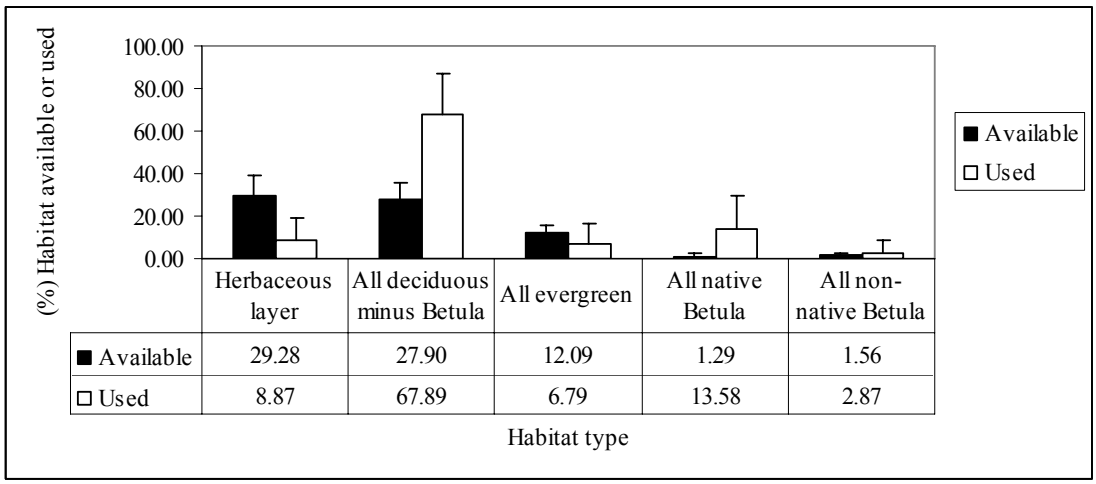
	Herbaceous layer	Deciduous tree	Evergreen tree	Deciduous shrub	Evergreen shrub
Available	29.28	18.32	6.75	12.42	5.34
Used	8.87	64.72	5.22	19.38	1.81

Figure 3.4 Blue tit foraging use relative to availability of focal tree and shrub genera in the CUBG where evergreen and deciduous *Quercus* and evergreen and deciduous *Prunus* plants have been combined respectively. All other plant genera were represented only by deciduous plants. Data have been averaged over all the blue tit nest (n = 11) boxes used in the compositional analyses.



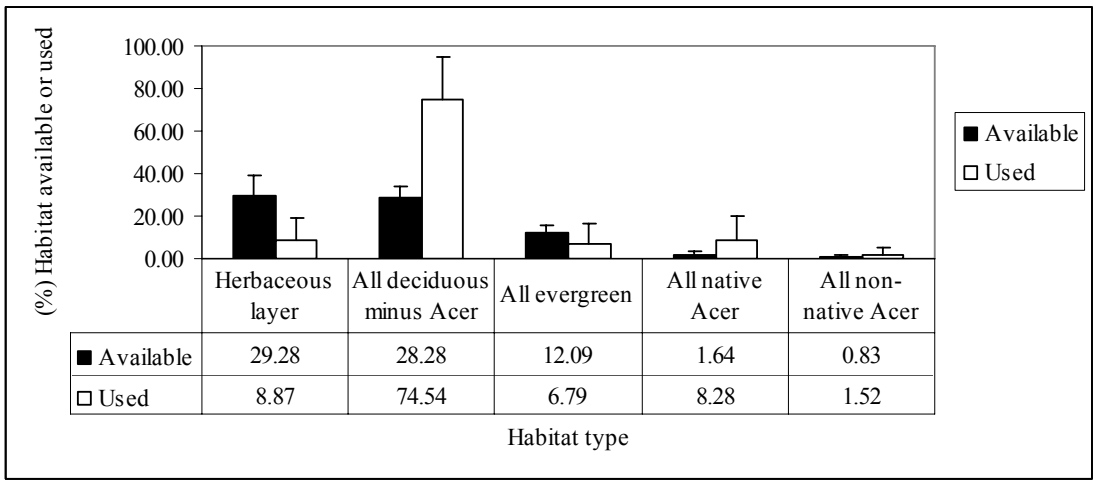
	Herbaceous layer	All other deciduous	All Quercus	All Prunus	All Acer	All Betula	All Populus	All Sorbus	All Fagus	All other evergreen
■ Available	29.28	17.03	2.51	2.61	2.46	2.85	2.30	1.39	1.12	10.57
□ Used	8.87	20.63	13.88	10.14	9.80	16.45	5.47	5.18	3.33	6.28

Figure 3.5 Blue tit foraging use relative to availability of the native and non-native *Betula* trees and shrubs available in the CUBG. Data have been averaged over all the blue tit nest boxes (n = 11) used in the compositional analyses.



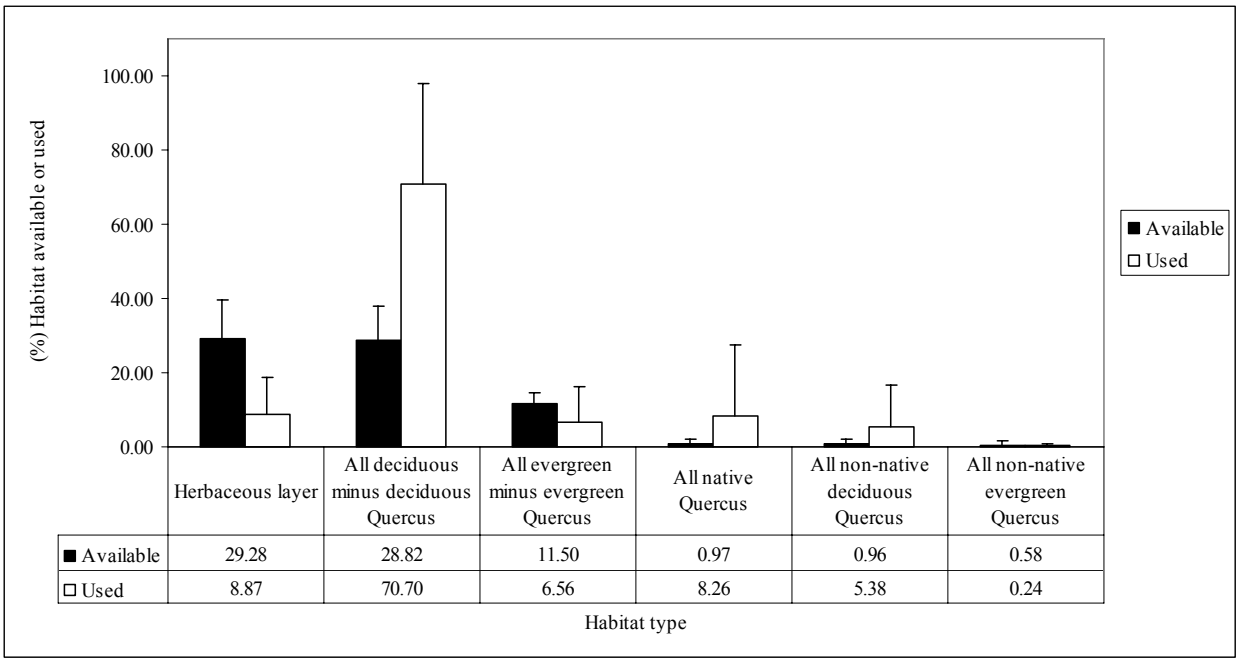
	Herbaceous layer	All deciduous minus Betula	All evergreen	All native Betula	All non-native Betula
■ Available	29.28	27.90	12.09	1.29	1.56
□ Used	8.87	67.89	6.79	13.58	2.87

Figure 3.6 Blue tit foraging use relative to availability of the native and non-native *Acer* trees and shrubs available in the CUBG. Data have been averaged over all the blue tit nest boxes (n = 11) used in the compositional analyses.



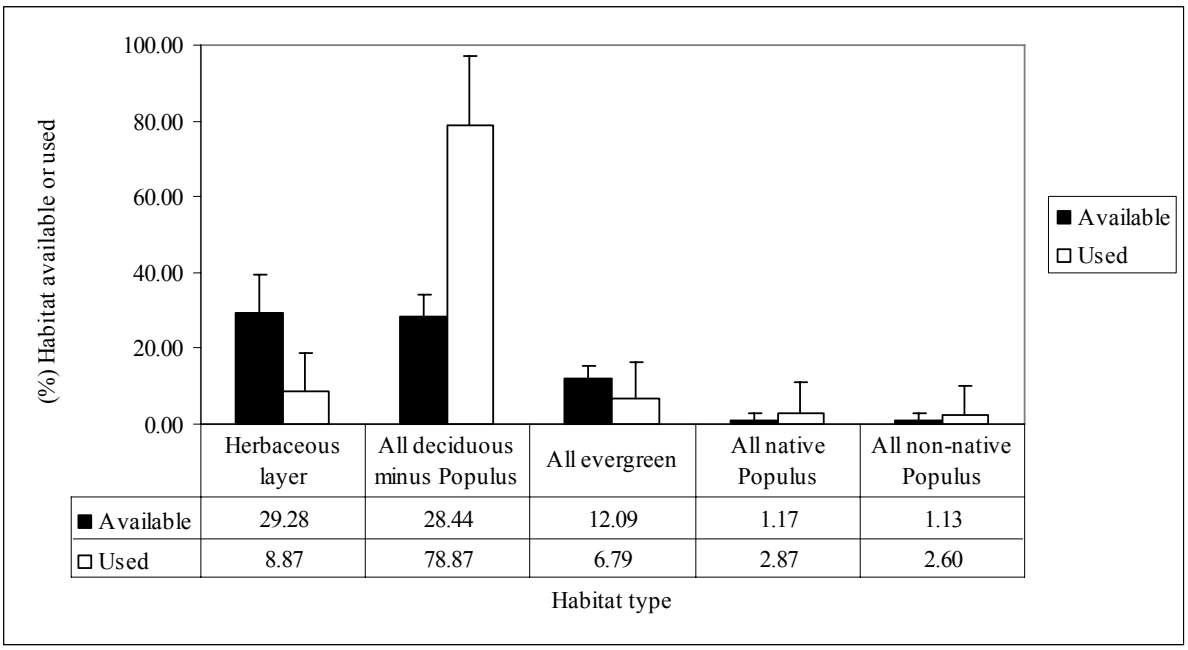
	Herbaceous layer	All deciduous minus Acer	All evergreen	All native Acer	All non-native Acer
Available	29.28	28.28	12.09	1.64	0.83
Used	8.87	74.54	6.79	8.28	1.52

Figure 3.7 Blue tit foraging use relative to availability of the native and non-native and evergreen and deciduous *Quercus* trees and shrubs available in the CUBG. Please note that all native *Quercus* trees and shrubs were deciduous. Data have been averaged over all the blue tit nest boxes (n = 11) used in the compositional analyses.



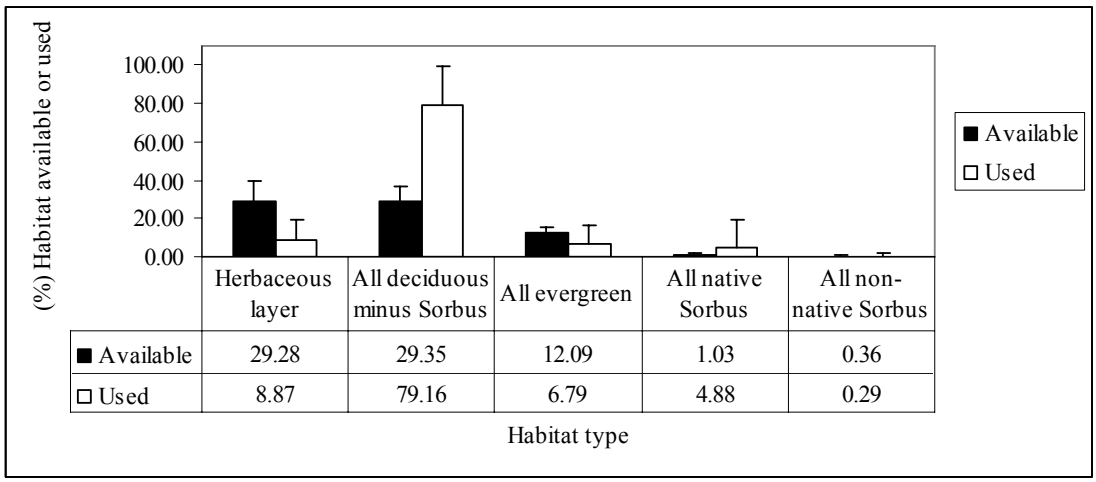
	Herbaceous layer	All deciduous minus deciduous Quercus	All evergreen minus evergreen Quercus	All native Quercus	All non-native deciduous Quercus	All non-native evergreen Quercus
■ Available	29.28	28.82	11.50	0.97	0.96	0.58
□ Used	8.87	70.70	6.56	8.26	5.38	0.24

Figure 3.8 Blue tit foraging use relative to availability of the native and non-native *Populus* trees and shrubs available in the CUBG. Data have been averaged over all the blue tit nest boxes (n = 11) used in the compositional analyses.



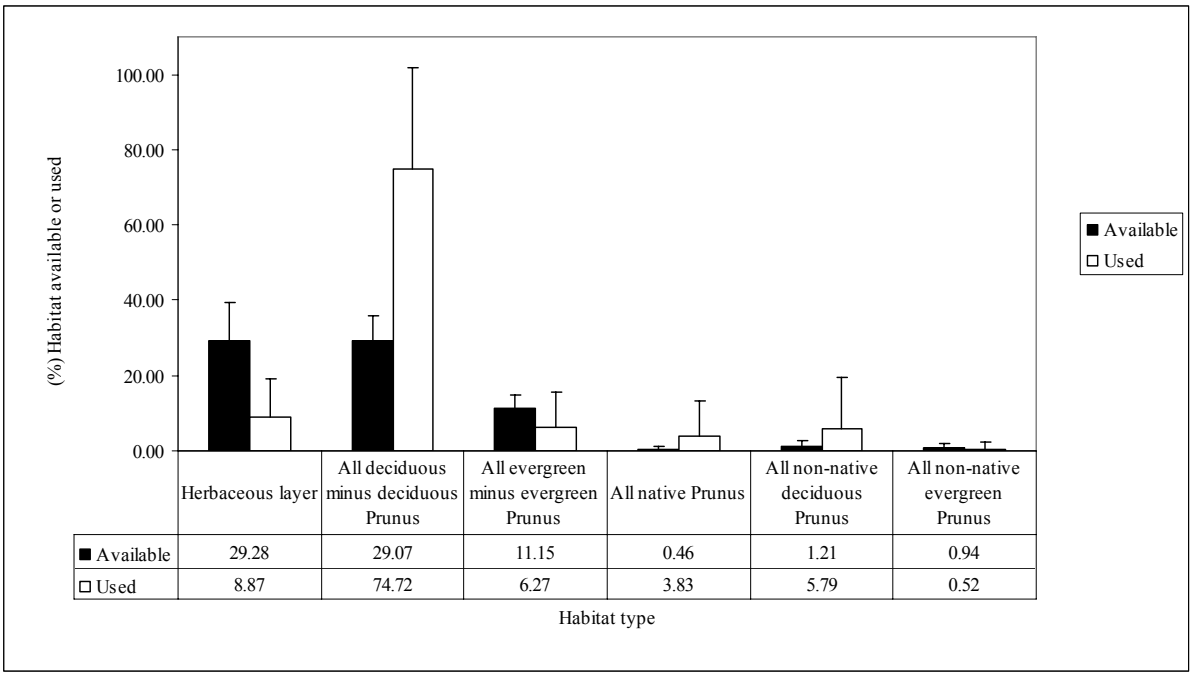
	Herbaceous layer	All deciduous minus Populus	All evergreen	All native Populus	All non-native Populus
Available	29.28	28.44	12.09	1.17	1.13
Used	8.87	78.87	6.79	2.87	2.60

Figure 3.9 Blue tit foraging use relative to availability of the native and non-native *Sorbus* trees and shrubs available in the CUBG. Data have been averaged over all the blue tit nest boxes (n = 11) used in the compositional analyses.



	Herbaceous layer	All deciduous minus Sorbus	All evergreen	All native Sorbus	All non-native Sorbus
■ Available	29.28	29.35	12.09	1.03	0.36
□ Used	8.87	79.16	6.79	4.88	0.29

Figure 3.10 Blue tit foraging use relative to availability of the native and non-native and evergreen and deciduous *Prunus* trees and shrubs available in the CUBG. Please note that all native *Prunus* trees and shrubs were deciduous. Data have been averaged over all the blue tit nest boxes (n = 11) used in the compositional analyses.



	Herbaceous layer	All deciduous minus deciduous Prunus	All evergreen minus evergreen Prunus	All native Prunus	All non-native deciduous Prunus	All non-native evergreen Prunus
Available	29.28	29.07	11.15	0.46	1.21	0.94
Used	8.87	74.72	6.27	3.83	5.79	0.52

Table 3.13 Compositional analysis tests (Wilk's lambda) and habitat rankings for foraging use by blue tits in various habitat types, obtained when a value of 0 from an available but un-utilised habitat type is replaced by 1, 0.1, 0.01, 0.001 and 0.0001% in turn. Statistical significance is denoted by the symbol >>> between two consecutively ranked habitat types; > denotes a non-significant difference and = denotes no difference. * denotes the default replacement value selected by the compositional analysis program and used in the main tests.

0% replaced by	Wilks Lambda	Randomisation *P*	Habitat rankings
a)	Where A = native/or n/c Europe trees and shrubs, B = Asia trees and shrubs, C = Americas trees and shrubs, D = Med/south Europe trees and shrubs, E = 'Other' trees and shrubs and F = herbaceous layer		
1%	0.221	0.001	A>>>E>B>D>C>>>F
0.1% *	0.298	0.002	A>>>B>C>D>E>F
0.01%	0.312	0.001	A>>>B>C>D>E>F
0.001%	0.314	0.001	A>>>B>C>D>F>E
0.0001%	0.315	0.001	A>>>B>C>D>F>E
b)	Where A = native deciduous tree and shrub, B = non-native deciduous tree and shrub, C = native evergreen tree and shrub, D = herbaceous layer and E = non-native evergreen tree and shrub		
1%	0.166	0.001	A>>>B>C>>>E>D
0.1% *	0.160	0.001	A>>>B>>>C>D>E
0.01%	0.151	0.001	A>>>B>>>D>E>C
0.001%	0.148	0.001	A>>>B>>>D>E>C
0.0001%	0.147	0.001	A>>>B>>>D>E>C
c)	Where A = deciduous tree, B = deciduous shrub, C = evergreen tree, D = herbaceous layer and E = evergreen shrub		
1%	0.141	0.001	A>>>B>>>C>E>D
0.1% *	0.111	0.001	A>>>B>>>C>D>E
0.01%	0.108	0.001	A>>>B>>>D>C>E
0.001%	0.111	0.001	A>>>B>>>D>C>E
0.0001%	0.115	0.001	A>>>B>>>D>C>E
d)	Where A = all *Betula* trees and shrubs, B = all other deciduous trees and shrubs, C = all *Acer* trees and shrubs, D = all *Populus* trees and shrubs, E = all *Quercus* trees and shrubs, F = all *Prunus* trees and shrubs, G = all *Sorbus* trees and shrubs, H = herbaceous layer, I = all *Fagus* trees and shrubs and J = all other evergreen trees and shrubs		
1%	0.118	0.002	A>D=C=E>G>F>I>B>>>J>H
0.1%	0.283	0.029	A>C>B>D>E>F>G>I>H>J
0.01%	0.308	0.067	A>B>C>D>E>F>G>H>I>J
0.001% *	0.271	0.046	A>B>C>D>E>F>G>H>I>J
0.0001%	0.238	0.026	A>B>C>D>F=E>H=G>J>I

Table 3.14 Compositional analysis tests (Wilk's lambda) and habitat rankings for foraging use by blue tits in different tree and shrub genera, obtained when a value of 0 from an available but un-utilised habitat type is replaced by 1, 0.1, 0.01, 0.001 and 0.0001% in turn. Statistical significance is denoted by the symbol >>> between two consecutively ranked habitat types; > denotes a non-significant difference and = denotes no difference. * denotes the default replacement value selected by the compositional analysis program and used in the main tests.

0% replaced by	Wilks Lambda	Randomisation *P*	Habitat rankings
a)	Where A = all deciduous trees and shrubs minus *Acer*, B = all native *Acer* trees and shrubs, C = herbaceous layer, D = all non-native *Acer* trees and shrubs and E = all evergreen trees and shrubs		
1%	0.190	0.001	B>A>D>>>E>C
0.1%	0.233	0.001	A>B>D>>>E>C
0.01%	0.217	0.001	A>>>B>D>C>E
0.001% *	0.202	0.001	A>>>B>C>D>E
0.0001%	0.192	0.001	A>>>B>C>E>D
b)	Where A = all native *Betula* trees and shrubs, B = all decid trees and shrubs minus *Betula*, C = all non-native *Betula* trees and shrubs, D = herbaceous layer and E = all evergreen trees and shrubs		
1%	0.148	0.002	A>>>B>C>>>E>D
0.1%	0.203	0.001	A>>>B>>>C>>>E>D
0.01%*	0.219	0.001	A>B>>>C>D>E
0.001%	0.225	0.001	A>B>>>C>D>E
0.0001%	0.227	0.001	A>B>>>D>C>E
c)	Where A = all deciduous trees and shrubs minus *Populus*, B = all native *Populus* trees and shrubs, C = herbaceous layer, D = all non-native *Populus* trees and shrubs and E = all evergreen trees and shrubs		
1%	0.167	0.003	B>A>D>E>C
0.1%	0.191	0.008	A>>>B>D>E>C
0.01%	0.185	0.012	A>>>B>C>D>E
0.001% *	0.178	0.013	A>>>B>C>D>E
0.0001%	0.172	0.006	A>>>C>B>D>E
d)	Where A = all deciduous trees and shrubs minus deciduous *Prunus* , B = all non-native deciduous *Prunus* trees and shrubs, C = herbaceous layer, D = all native *Prunus* trees and shrubs, E = all evergreen trees and shrubs minus evergreen *Prunus* and F = all non-native evergreen *Prunus* trees and shrubs		
1%	0.079	0.001	B>D>>>A>F>>>E>C
0.1%	0.237	0.001	A>B>D>F>C>E
0.01%	0.201	0.001	A>>>B>D>C>F>E
0.001% *	0.168	0.001	A>>>B>C>D>E>F
0.0001%	0.150	0.001	A>>>B>C>D>E>F
e)	Where A = all deciduous trees and shrubs minus deciduous *Quercus* , B = all native *Quercus* trees and shrubs, C = all non-native deciduous *Quercus* trees and shrubs, D = all non-native evergreen *Quercus* trees and shrubs, E = herbaceous layer and F = all evergreen trees and shrubs minus evergreen *Quercus*		
1%	0.088	0.001	C>B>D>A>>>F>E
0.1%	0.164	0.002	A>C>B>D>>>E>F
0.01%	0.191	0.005	A>>>C>B>D>E>F
0.001% *	0.200	0.005	A>B>C>D>E>F
0.0001%	0.202	0.004	A>B>C>E>D>F
f)	Where A = all deciduous trees and shrubs minus *Sorbus*, B = herbaceous layer, C = all native *Sorbus* trees and shrubs, D = all evergreen trees and shrubs and E = all non-native *Sorbus* trees and shrubs		
1%	0.170	0.001	E>C>A>>>D>B
0.1%	0.162	0.001	A>>>C>E>D>B
0.01%	0.108	0.001	A>>>C>B=D=E
0.001% *	0.089	0.001	A>>>B>C>D>E
0.0001%	0.081	0.001	A>>>B>D>C>E

3.3.2 Blue tit and great tit foraging preferences in the Botanic Gardens

Blue tit and great tit foraging preferences were analysed in the whole of the (sampled) CUBG using two-way G tests and goodness-of-fit chi-square tests. I used two-way G tests to test for variation between the breeding seasons of 2006-2008 for both blue tits and great tits to see whether it would be correct to pool the data, the results of which can be seen in Tables 3.15 (for blue tits) and 3.16 (for great tits). All of the tests for great tits were non-significant; meaning no difference between years, so all data was pooled. The majority of the tests for blue tits were non-significant and so I also pooled the data across breeding seasons for blue tits. However, either one or two out of the six tests conducted on each habitat type for blue tits (Table 13.5a-f) were significant. This indicated that blue tits may have been more variable in their foraging across breeding seasons than great tits. In order to test this, I split years for blue tits to test their foraging use of native and non-native trees and shrubs, the results of which can be seen further below (section *3.3.2.3*).

3.3.2.1 Blue tit foraging use over all seasons

Table 3.17 shows the results from chi-square tests that examined blue tit habitat use over the whole breeding season, with 2006-2008 data pooled. From this Table, blue tits are shown to differ significantly in their use of native (and northern/central European) and non-native trees and shrubs (3.17a), of native and non-native trees (3.17b), of trees, shrubs and herbaceous layers (3.17d) and of evergreen and deciduous trees and shrubs (3.17f). Figures 3.11-3.14 showing the observed and expected frequencies (the expected values having been calculated from % availability of the total sampled vegetation within the CUBG) of the highest and lowest P values reported in Table 3.17 can be used to determine the pattern of the foraging use in the significant tests above; blue tits were

observed more than expected by chance in native trees and shrubs (Figure 3.11) and native trees (Figure 3.12) and observed less than expected in non-natives. They were observed more than expected in trees, but not in shrubs, and they were observed foraging much less than expected in the herbaceous layer given the availability of this habitat (Figure 3.13) suggesting their plant preference is for trees and that herbaceous layers were the least preferred. Blue tits were observed more than expected in deciduous trees and shrubs and observed less than expected in evergreen trees and shrubs (Figure 3.14).

Four out of the six tests examining blue tit use of native and non-native shrubs were significant (Table 3.17c) and although two weren't significant, Figure 3.15 shows that the observed and expected frequencies from the highest (and non-significant) P value followed a similar pattern to the observed and expected frequencies of the lowest (and significant) P value. This pattern found blue tits to be observed in native shrubs more than expected and less than expected in non-native shrubs, again suggesting a preference for natives.

Plant use was examined omitting herbaceous layers and only considering blue tit foraging use of trees and shrubs. Five out of these tests were found to be significant (Table 3.17e) with again the observed and expected frequencies of the highest (non-significant) P value following a similar pattern to the observed and expected frequencies of the lowest (and significant) P value, i.e. blue tits were observed more than expected in trees and observed less than expected in shrubs (Figure 3.16) suggesting that trees (as in Table 3.17d) were still the preferred plant to forage in by blue tits.

3.3.2.2 Blue tit foraging split by different breeding periods

Table 3.18 shows the results from chi-square tests that examined blue tit foraging use in different periods of the breeding season: period one - nest building/egg laying/incubation, period two - chick feeding and period three – fledging. As above, all data were pooled across breeding seasons. All of the test results examining blue tit foraging use of native and non-native trees and shrubs (Table 3.18a) and native and non-native trees (Table 3.18b) during each breeding period were significant. This suggests that native plants were preferred over non-natives in all breeding periods. However, when shrubs were analysed separately, it was found that none of the tests were significant during breeding period two (chick feeding) and only one of the tests was significant during breeding period three (fledging) (Table 3.18c). The origin of shrubs therefore appears to become less important to the blue tit during these two periods than in breeding period one (nest building/egg laying/incubation), where all six of the tests were significant. This is further demonstrated in Figure 3.17; the observed frequencies of the highest (and non-significant) P values in breeding period two and breeding period three in both native and non-native shrubs rarely differ from the expected frequencies. The tests resulting in the lowest P values in breeding periods two and three do show a tendency for native shrubs to be used more than expected and non-native shrubs to be used less than expected, but the majority of tests are not significant and this pattern is not very strong.

During breeding periods one and two, blue tits were observed foraging in trees more than expected (Figure 3.18), with five out of the six tests conducted on each of these breeding periods being significant (Table 3.18d). However, during breeding period three, although Figure 3.18 shows a tendency for blue tits to be using trees more than expected and shrubs less than expected, none of the six tests were significant. Therefore,

when they are feeding their fledglings outside of the next box, the type of plant (tree or shrub) becomes less important to them.

Blue tit avoidance of evergreen foliage (Table 3.18e) during the different breeding periods rarely differs, with only one test being non-significant during breeding period two, suggesting their preference for deciduous plants over evergreen ones (as shown in Figure 3.14) is consistent over the whole breeding season.

3.3.2.3 Blue tit foraging split by different years

I tested these differences by looking at blue tit foraging use in native and non-native trees and shrubs. From Table 3.19 it can be seen that during 2006 only half of the chi-square tests were significant compared with all of the tests being significant in the 2007 and 2008 breeding seasons. The pattern from all of the tests, including the non-significant ones shows that blue tits were observed foraging in native trees and shrubs more than expected and were observed less in non-native trees and shrubs than expected (Figure 3.19). However, since half the tests in 2006 were non-significant this pattern of use was not as strong as in 2007 and 2008.

3.3.2.4 Great tit foraging use over all seasons

Table 3.20 shows the results from chi-square tests that examined great tit foraging use over the whole breeding season, with 2006-2008 data pooled. From this Table, great tits are shown not to differ significantly in any of the tests of their use of native (and northern European) and non-native trees and shrubs (3.20a), of native and non-native trees (3.20b), of native and non-native shrubs (3.20c) and of evergreen and deciduous trees and shrubs (3.20f). Figures 3.20-3.23 showing the observed and expected

frequencies of the highest and lowest P values (out of six) from the chi-square test reported in Table 3.20 can be used to determine the pattern of the foraging use in the tests above; in the highest reported P value, great tits were observed more or less equally in native and non-native trees and shrubs (Figure 3.20). In these tests great tits show a tendency to use native trees and shrubs more than expected and non-native trees and shrubs less than expected but this difference is only slight and not significant. This pattern is repeated in Figure 3.21 with foraging great tits being observed slightly more on native trees than expected and slightly less on non-natives than expected but again this difference is too slight to draw any conclusions. However, when looking at great tit foraging use of native and non-native shrubs (Figure 3.22), the lowest P value (out of six) from the chi-square test shows the opposite pattern with great tits being observed more than expected on non-native shrubs and less than expected on native shrubs. The highest P value test shows virtually no difference between observed and expected frequencies of use on native shrubs and non-native shrubs. Great tits therefore do not appear to discriminate between the use of native and non-native shrubs within the garden, with a slight tendency to use native trees more than non-native trees, although not significantly so.

Examining leaf type, from the highest P value test great tits were observed to use deciduous trees and shrubs and evergreen trees and shrubs virtually as expected from their availability (Figure 3.23). The lowest P value test shows a tendency for them to forage in deciduous trees and shrubs more than expected and forage less than expected in evergreen trees and shrubs but being non-significant it appears that great tits do not have a strong preference for deciduous over evergreen plants.

Looking at great tit foraging use of plant type, four out of six of chi-square tests testing for use of trees, shrubs and herbaceous layers were significant (Table 3.20d). From

Figure 3.24 it can be seen that this difference probably lies in their use of herbaceous layers with the observed frequencies being much less than expected in both the highest and lowest P values compared with tree use where great tits were observed in trees more than expected. When herbaceous layers were taken out of the test, the tests became less significant with only two out of the six tests testing for foraging use in trees against shrubs being significant (Table 3.20e). From Figure 3.25 the highest (and non-significant) P value shows great tits being observed slightly less than expected in trees and slightly more than expected in shrubs. However this pattern is reversed in the lowest (and significant) P value. It is therefore difficult to draw any conclusions on great tit plant use except that they appear to forage in herbaceous layers the least compared with herbaceous layer availability.

3.3.2.5 Great tit foraging split by different breeding periods

Table 3.21 shows the results from chi square tests that examined great tit foraging use in different periods of the breeding season. As above, all data were pooled across breeding seasons. Great tits differed in their use of native and non-native trees and shrubs during breeding period one (nest building/egg laying/incubation), where three out of six of the tests were significant compared with none of the tests being significant in breeding periods two (chick feeding) and three (fledging) (Table 3.21a). By splitting native and non-native trees and shrubs it became clear that these differences lay in their use of trees (Table 3.21b) rather than shrubs, which (in shrubs) resulted in all tests becoming non-significant and indicating a preference for neither native nor non-native (Table 3.21c). By removing shrubs from the analysis, during breeding period one, five out of six of the tests testing origin use in trees were significant (Table 3.21b) and Figure 3.26 shows that great tits were observed using native trees more than expected and using non-native trees less than expected. Interestingly this pattern is reversed during breeding period

three with the non-native trees being used more than expected, with two out of the six tests in this breeding period now becoming significant (Table 3.21b). Thus origin in shrubs appears to be unimportant to great tits during all periods and native trees are only used preferentially when the adults are nest building/egg laying/incubating.

In breeding periods one and three great tits do not differ in their use of trees and shrubs, with all tests being non-significant (Table 3.21d), observed and expected frequencies being very similar (Figure 3.27). However, in breeding period two all tests were significant and from Figure 3.27 great tits can be seen to be using trees more than expected and shrubs less than expected. They therefore appear make a switch to using trees during the chick feeding period.

As found when pooling the breeding periods and reported above (Table 3.20f) great tits use of deciduous and evergreen trees and shrubs was found to be non-significant within each breeding period in all tests (Table 3.21e). They are therefore not discriminating between particular leaf types and appear to be foraging non-selectively in evergreen and deciduous trees and shrubs.

Table 3.15 Two-way G tests (likelihood ratio test) comparing year against the observed and expected frequencies of blue tit foraging use in various habitat types. The table shows the result of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. 'Origin' refers to a plant being either a native (including northern and central European) or a non-native (Americas, Asia, Med/south Europe and 'Other'). *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$.

Test	Number of tests which are significant (out of 6)	*df*	X^2 test of lowest P value		X^2 test of lowest P value	
			X^2	*N*	X^2	*N*
Year by:						
a) Origin (trees and shrubs)	1/6	2	0.598	73	7.779*	69
b) Origin (trees)	2/6	2	1.537	72	8.764*	73
c) Origin (shrubs)	1/6	2	1.234	59	6.971*	58
d) Plant type (trees, shrubs and herbaceous layer)	2/6	4	1.842	73	11.903*	72
e) Plant type (trees and shrubs)	2/6	2	0.121	73	9.995**	69
f) Leaf type (evergreen and deciduous)	1/6	2	0.033	73	11.004**	70

Table 3.16 Two-way G tests (likelihood ratio test) comparing year against the observed and expected frequencies of great tit foraging use in various habitat types. The table shows the result of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. 'Origin' refers to a plant being either a native (including northern and central European) or a non-native (Americas, Asia, Med/south Europe and 'Other'). *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$.

Test	Number of tests which are significant (out of 6)	*df*	X^2 test of lowest P value		X^2 test of lowest P value	
			X^2	*N*	X^2	*N*
Year by:						
a) Origin (trees and shrubs)	0/6	2	0.557	35	5.766	34
b) Origin (trees)	0/6	2	0.223	40	2.356	40
c) Origin (shrubs)	0/6	2	0.291	29	5.191	29
d) Plant type (trees, shrubs and herbaceous layer)	0/6	4	2.007	45	4.824	45
e) Plant type (trees and shrubs)	0/6	2	0.079	35	2.528	37
f) Leaf type (evergreen and deciduous)	0/6	2	0.219	35	4.631	37

Table 3.17 Chi-square goodness-of-fit tests comparing observed and expected frequencies of use of various habitat types by blue tits. The table shows the result of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$.

Test	Number of tests which are significant (out of 6)	*df*	χ^2 test of highest P value		χ^2 test of lowest P value	
			χ^2	*N*	χ^2	*N*
a) Native vs non-native trees & shrubs	6/6	1	5.606*	70	25.381***	73
b) Native vs non-native trees	6/6	1	10.263**	72	13.579***	72
c) Native vs non-native shrubs	4/6	1	1.698	59	17.004***	58
d) Trees vs shrubs vs herbaceous layer	6/6	2	35.198***	76	69.660***	71
e) Trees vs shrubs	5/6	1	1.780	70	19.623***	69
f) Evergreen vs deciduous	6/6	1	09.748**	70	21.564***	70

Table 3.18 Chi-square goodness-of-fit tests comparing observed and expected frequencies of use of various habitat types by blue tits in three different breeding periods (period one = nesting/egg laying/incubation, period two = chick feeding and period three = fledging). The table shows the result of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$.

	Test	Number of tests which are significant (out of 6)	*df*	χ^2 test of highest P value		χ^2 test of lowest P value	
				χ^2	*N*	χ^2	*N*
a)	Native vs non-native trees & shrubs						
	Breeding period one	6/6	1	12.319***	62	29.049***	59
	Breeding period two	6/6	1	4.491*	55	16.791***	53
	Breeding period three	6/6	1	6.763*	51	20.446***	50
b)	Native vs non-native trees						
	Breeding period one	6/6	1	11.915***	60	20.309***	60
	Breeding period two	6/6	1	4.250*	52	11.154***	51
	Breeding period three	6/6	1	6.114*	49	12.251***	48
c)	Native vs non-native shrubs						
	Breeding period one	6/6	1	6.086*	47	20.174***	47
	Breeding period two	0/6	1	0.015	31	1.150	30
	Breeding period three	1/6	1	0.047	34	8.958**	34
d)	Trees vs shrubs						
	Breeding period one	5/6	1	1.195	62	10.126**	59
	Breeding period two	5/6	1	2.181	55	8.117**	55
	Breeding period three	0/6	1	0.150	50	4.071	49
e)	Evergreen vs deciduous						
	Breeding period one	6/6	1	20.123***	62	25.248***	62
	Breeding period two	5/6	1	3.454	52	10.650**	51
	Breeding period three	6/6	1	6.738**	50	14.410***	50

Table 3.19 Chi-square goodness-of-fit tests comparing observed and expected frequencies of use of various habitat types by blue tits in three different breeding seasons (2006-2008). The table shows the result of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$.

Test	Number of tests which are significant (out of 6)	*df*	χ^2 test of highest P value		χ^2 test of lowest P value	
			χ^2	*N*	χ^2	*N*
Native vs non-native trees & shrubs						
2006	3/6	1	1.108	33	13.251***	35
2007	6/6	1	5.189*	44	16.123***	41
2008	6/6	1	10.635**	33	20.621***	34

Figure 3.11 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit foraging use of native (including northern and central Europe) and non-native (Americas, Asia, Med/south Europe and 'Other') trees and shrubs. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.17a for the significance level of these P values.

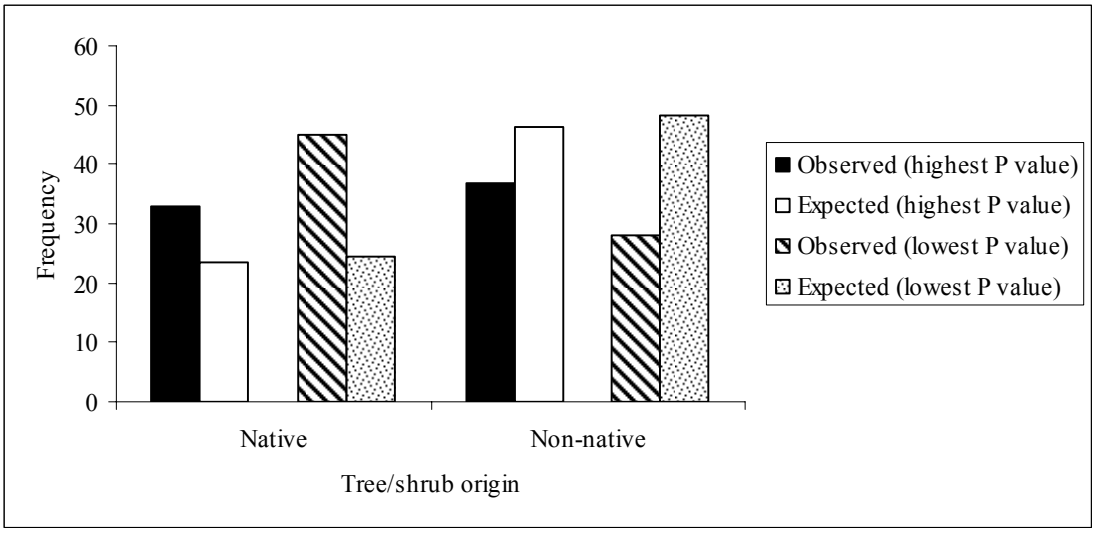


Figure 3.12 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit foraging use of native (including northern and central Europe) and non-native (Americas, Asia, Med/south Europe and 'Other') trees. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.17b for the significance level of these P values.

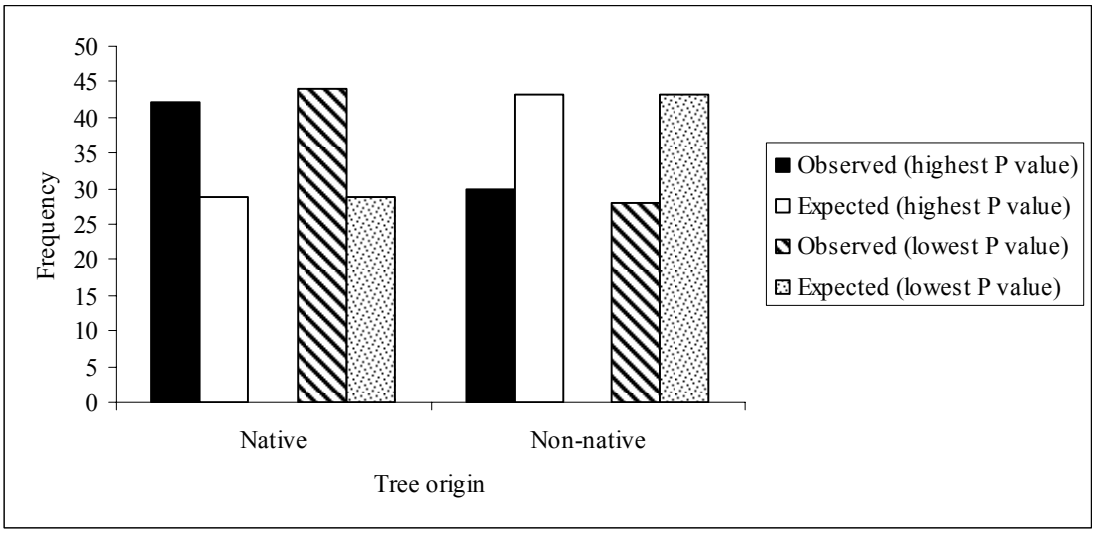


Figure 3.13 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit foraging use of different plant types (trees, shrubs or herbaceous layers). The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.17d for the significance level of these P values.

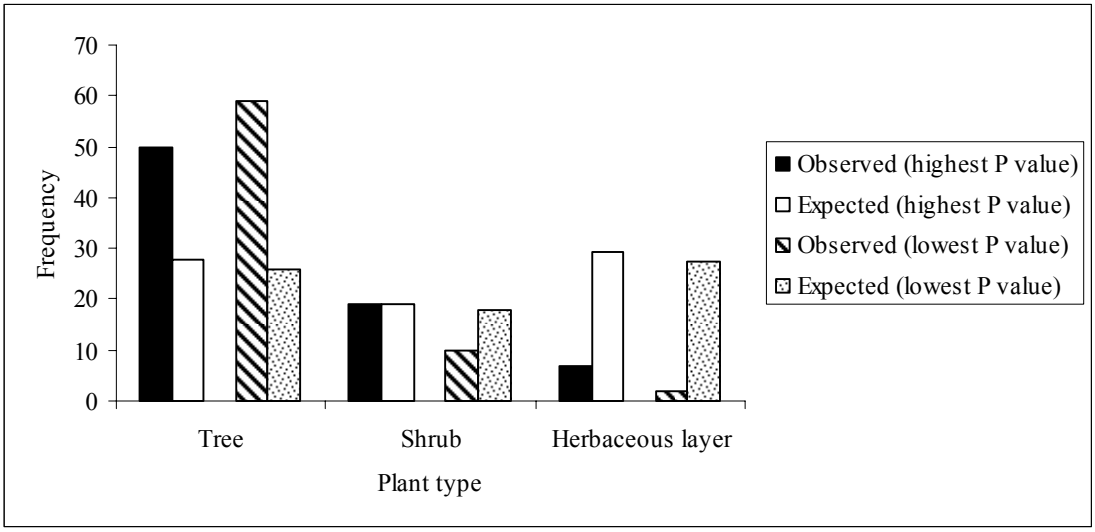


Figure 3.14 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit foraging use of different tree and shrub leaf types (evergreen or deciduous). The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.17f for the significance level of these P values.

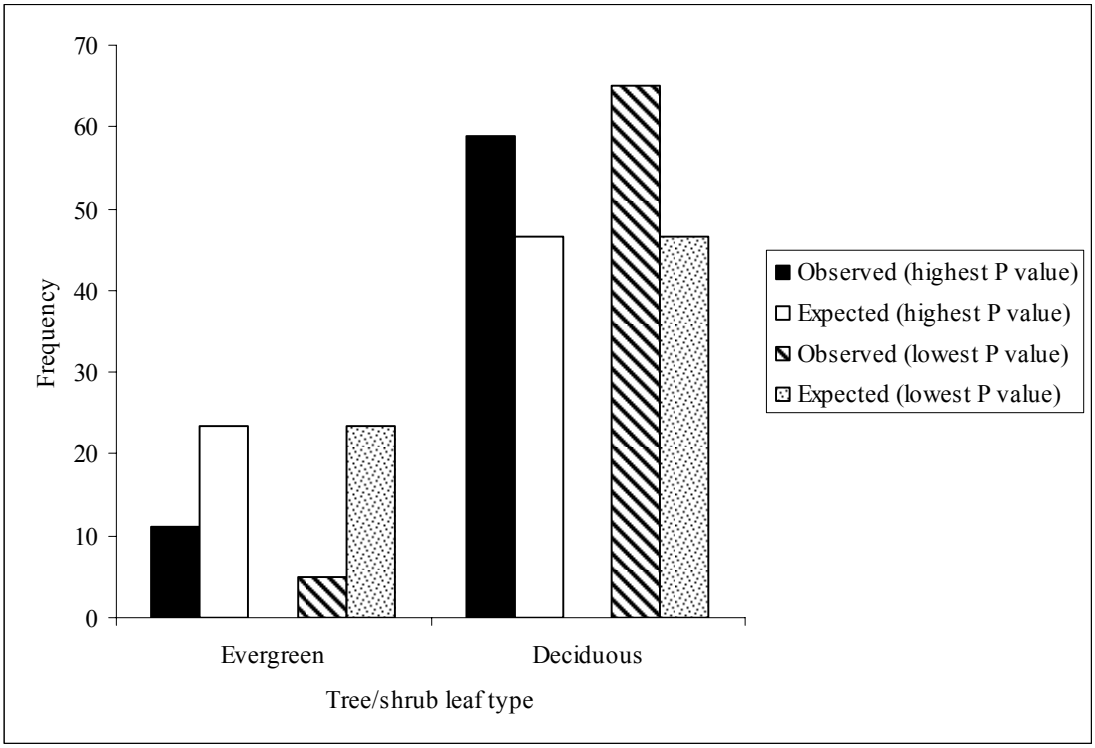


Figure 3.15 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit foraging use of native (including northern and central Europe) and non-native (Americas, Asia, Med/south Europe and 'Other') shrubs. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.17c for the significance level of these P values.

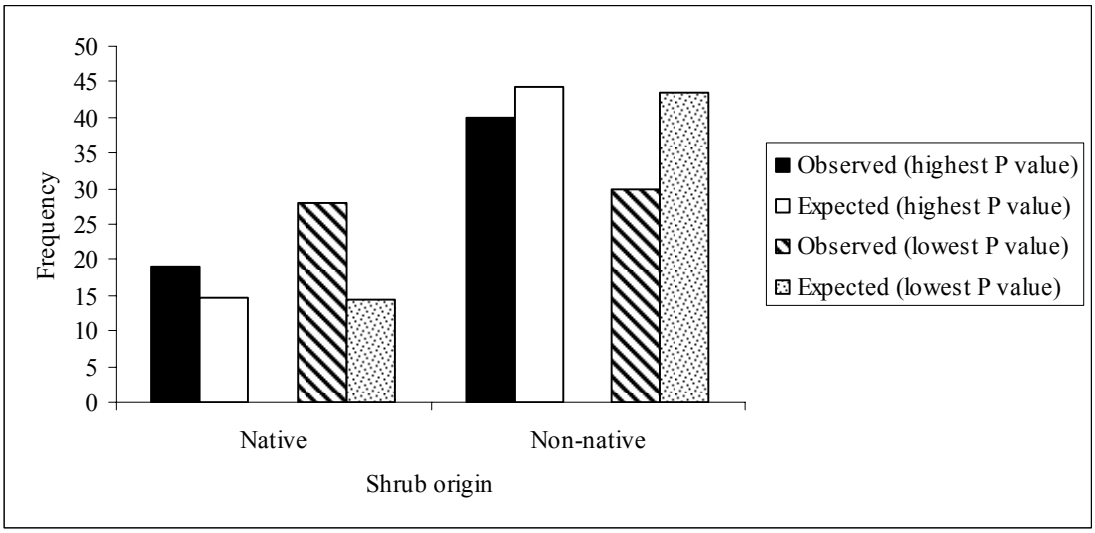


Figure 3.16 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit foraging use of different plant types (trees or shrubs). The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.17e for the significance level of these P values.

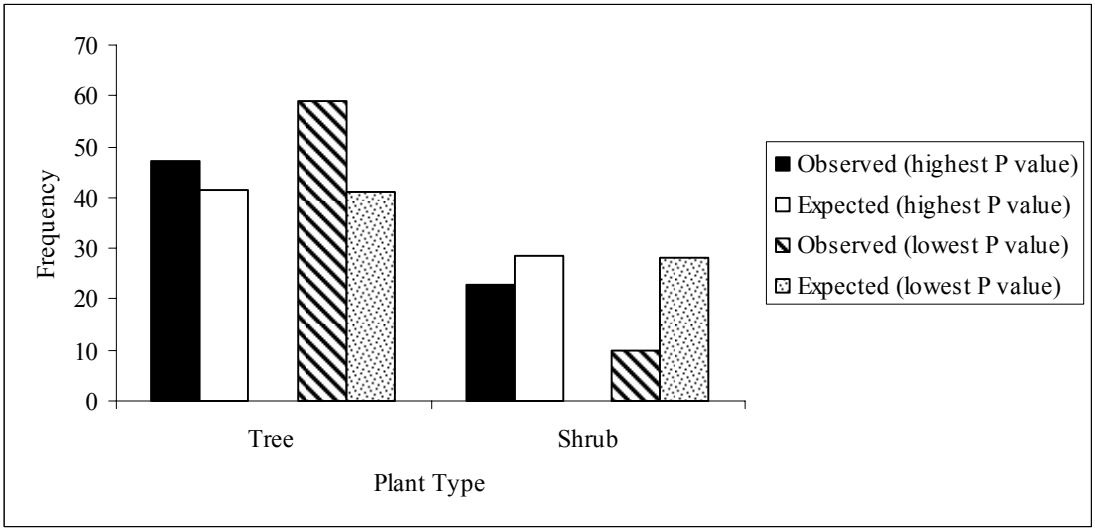


Figure 3.17 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit foraging use of native (including northern and central Europe) and non-native (Americas, Asia, Med/south Europe and 'Other') shrubs in three different breeding periods (period one = nesting/egg laying/incubation, period two = chick feeding and period three = fledging). The figure shows the results of the highest and lowest P values obtained from six repeated tests for each breeding period, with each test using an individual bird selected by a different random number. Significance levels for each P value for each of these tests are indicated by a solid line for the highest P value and a dashed line for the lowest P value. NS indicates a non-significant test result, * indicates a significant test result at $P \leq 0.05$ and ** indicates a significant test result at $P \leq 0.001$.

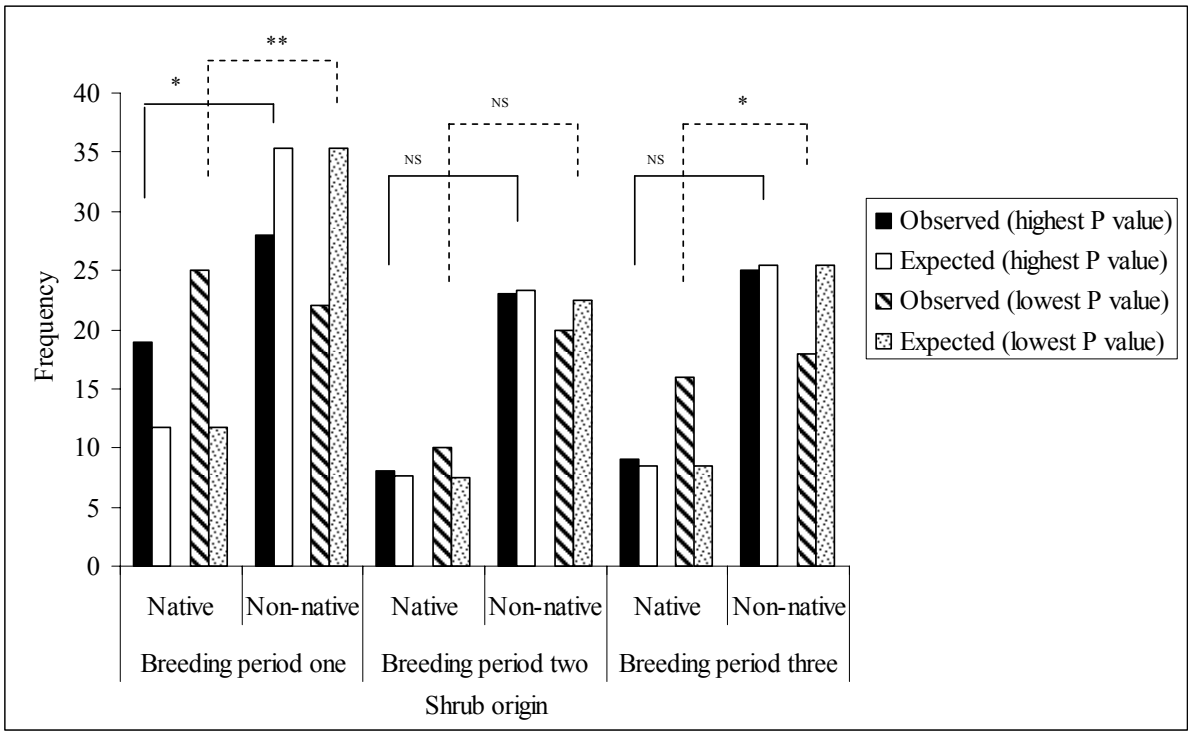


Figure 3.18 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit of different plant types (trees or shrubs) in three different breeding periods (period one = nesting/egg laying/incubation, period two = chick feeding and period three = fledging). The figure shows the results of the highest and lowest P values obtained from six repeated tests for each breeding period, with each test using an individual bird selected by a different random number. Significance levels for each P value for each of these tests are indicated by a solid line for the highest P value and a dashed line for the lowest P value. NS indicates a non-significant test result, * indicates a significant test result at $P \leq 0.05$ and ** indicates a significant test result at $P \leq 0.001$.

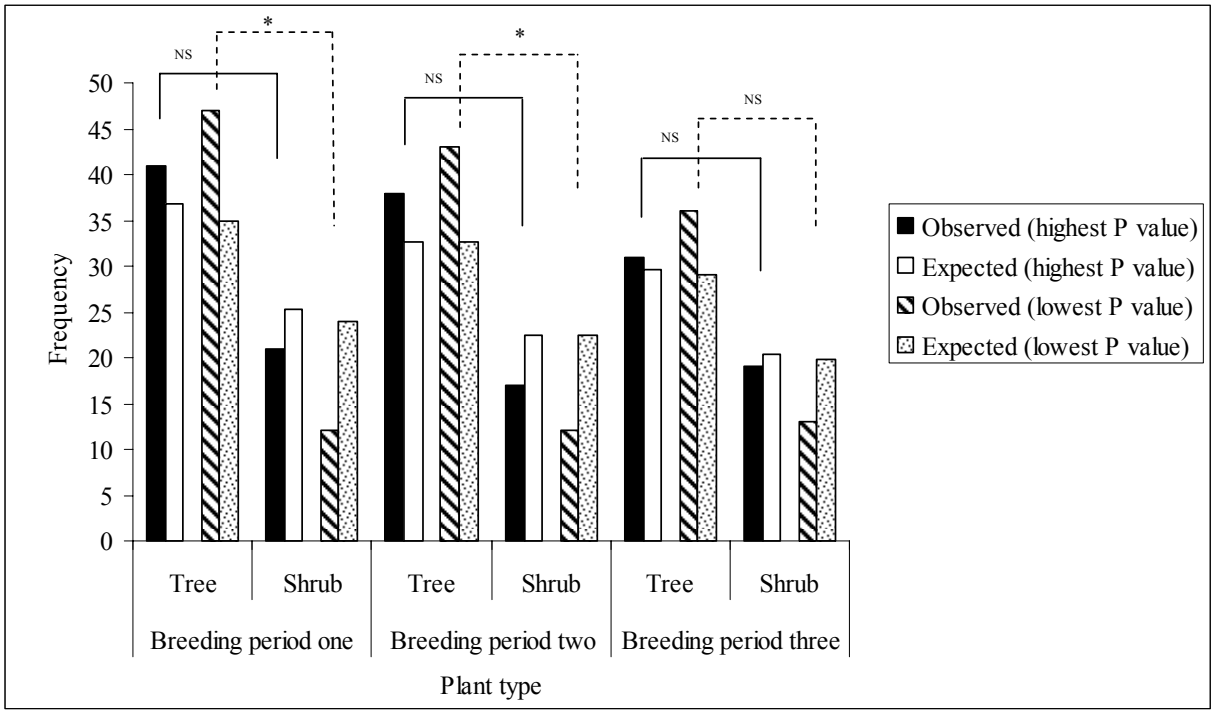


Figure 3.19 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit foraging use of native (including northern and central Europe) and non-native (Americas, Asia, Med/south Europe and 'Other') trees and shrubs in three different breeding seasons (2006-2008). The figure shows the results of the highest and lowest P values obtained from six repeated tests for each year, with each test using an individual bird selected by a different random number. Significance levels for each P value for each of these tests are indicated by a solid line for the highest P value and a dashed line for the lowest P value. NS indicates a non-significant test result, * indicates a significant test result at $P \leq 0.05$ and ** indicates a significant test result at $P \leq 0.001$.

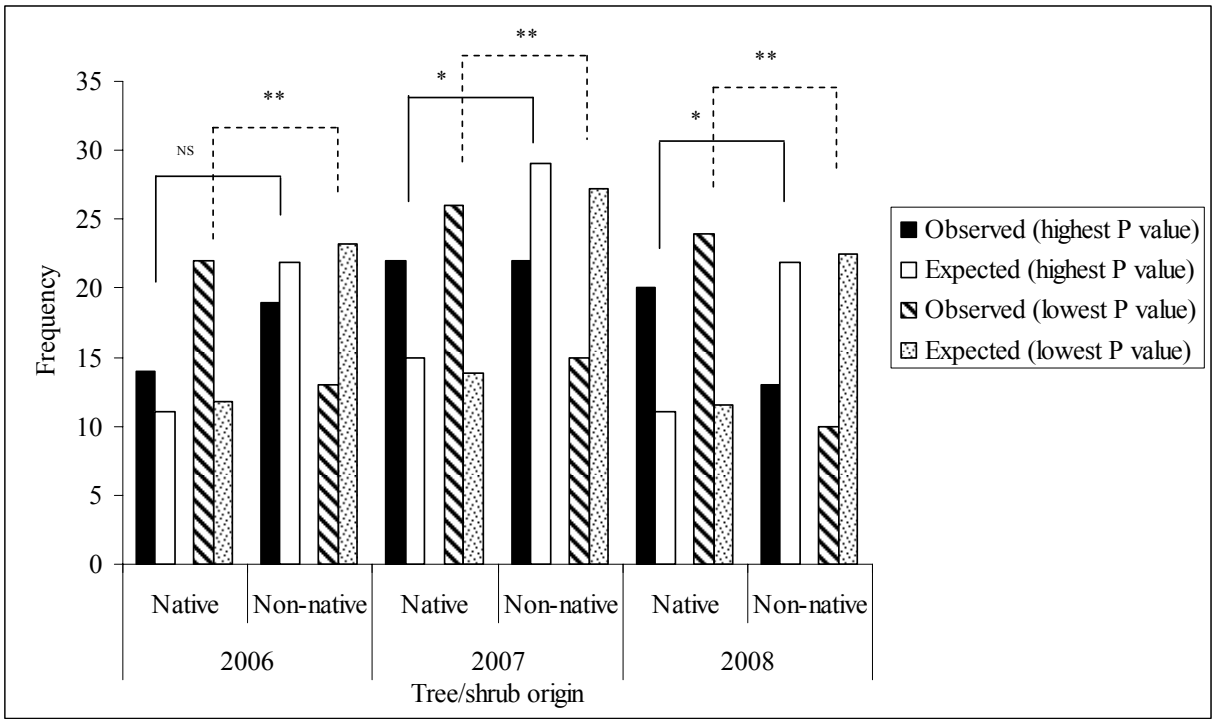


Table 3.20 Chi-square goodness-of-fit tests comparing observed and expected frequencies of use of various habitat types by great tits. The table shows the result of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$.

Test	Number of tests which are significant (out of 6)	*df*	χ^2 test of highest P value		χ^2 test of lowest P value	
			χ^2	*N*	χ^2	*N*
a) Native vs non-native trees & shrubs	0/6	1	0.029	34	0.764	37
b) Native vs non-native trees	0/6	1	0.159	42	1.719	40
c) Native vs non-native shrubs	0/6	1	0.008	29	3.275	29
d) Trees vs shrubs vs herbaceous layer	4/6	2	5.398	42	20.729***	42
e) Trees vs shrubs	2/6	1	0.366	35	5.575*	37
f) Evergreen vs deciduous	0/6	1	0.013	37	3.446	37

Table 3.21 Chi-square goodness-of-fit tests comparing observed and expected frequencies of foraging use of various habitat types by great tits in three different breeding periods (period one = nesting/egg laying/incubation, period two = chick feeding and period three = fledging). The table shows the result of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$.

	Test	Number of tests which are significant (out of 6)	*df*	χ^2 test of highest P value		χ^2 test of lowest P value	
				χ^2	*N*	χ^2	*N*
a)	Native vs non-native trees & shrubs						
	Breeding period one	3/6	1	0.971	23	8.716**	18
	Breeding period two	0/6	1	0.056	25	3.066	26
	Breeding period three	0/6	1	0.226	24	1.327	26
b)	Native vs non-native trees						
	Breeding period one	5/6	1	4.240	23	8.473**	23
	Breeding period two	0/6	1	0.000	30	0.943	31
	Breeding period three	2/6	1	1.143	24	5.381*	24
c)	Native vs non-native shrubs						
	Breeding period one	0/6	1	0.068	18	1.563	17
	Breeding period two	0/6	1	0.127	10	0.277	10
	Breeding period three	0/6	1	0.000	20	2.367	20
d)	Trees vs shrubs						
	Breeding period one	0/6	1	0.023	23	1.257	23
	Breeding period two	6/6	1	5.174*	23	13.723***	29
	Breeding period three	0/6	1	0.009	24	0.398	26
e)	Evergreen vs deciduous						
	Breeding period one	0/6	1	0.185	24	1.107	22
	Breeding period two	0/6	1	0.185	24	2.077	29
	Breeding period three	0/6	1	0.185	24	2.317	26

Figure 3.20 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing great tit foraging use of native (including northern and central Europe) and non-native (Americas, Asia, Med/south Europe and 'Other') trees and shrubs. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.20a for the significance level of these P values.

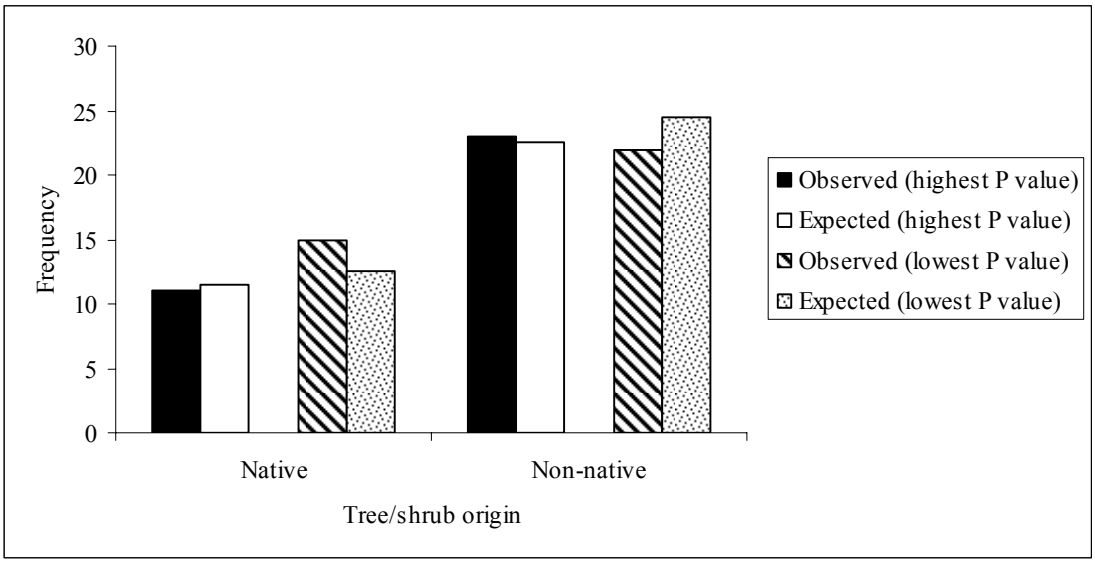


Figure 3.21 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing great tit foraging use of native (including northern and central Europe) and non-native (Americas, Asia, Med/south Europe and 'Other') trees. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.20b for the significance level of these P values.

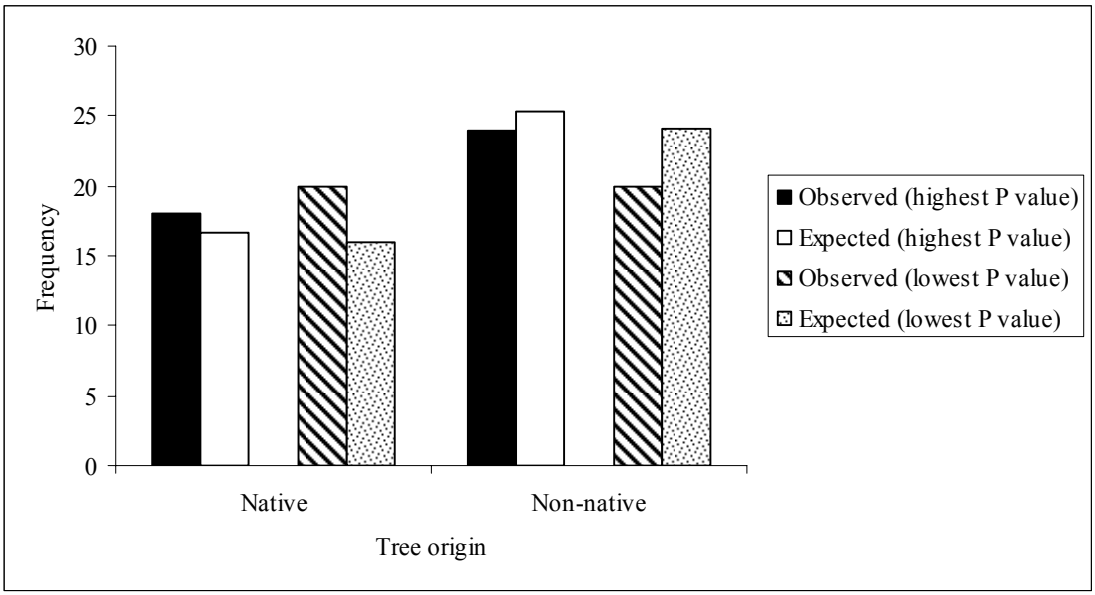


Figure 3.22 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing great tit foraging use of native (including northern and central Europe) and non-native (Americas, Asia, Med/south Europe and 'Other') shrubs. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.20c for the significance level of these P values.

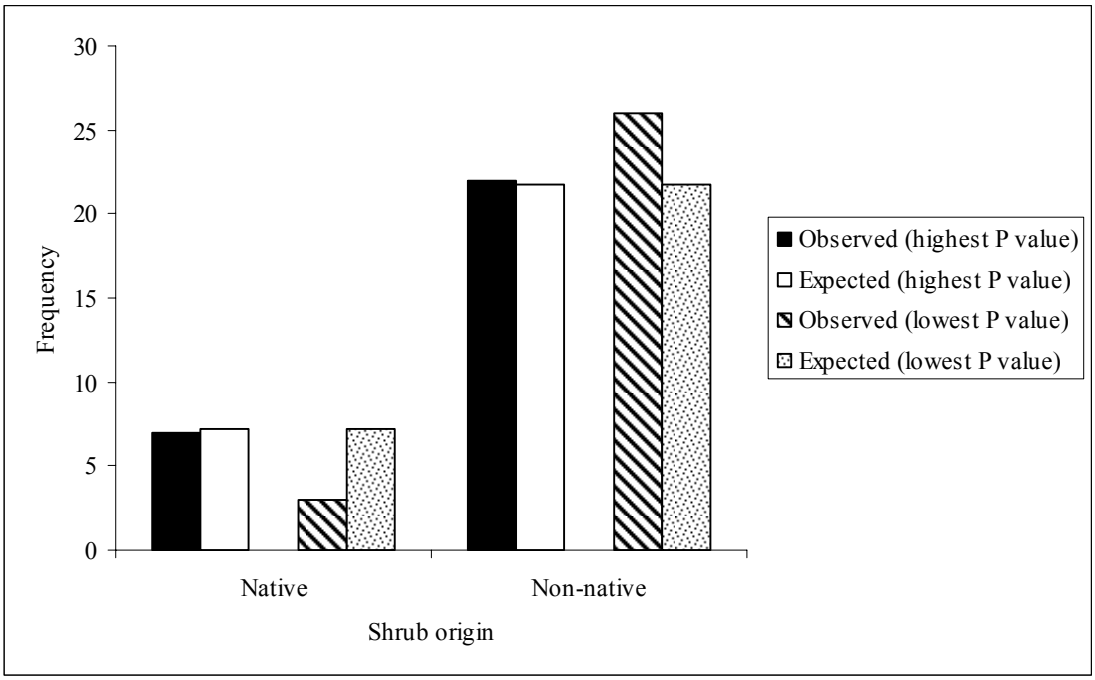


Figure 3.23 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing great tit foraging use of different tree and shrub leaf types (evergreen or deciduous). The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.20f for the significance level of these P values.

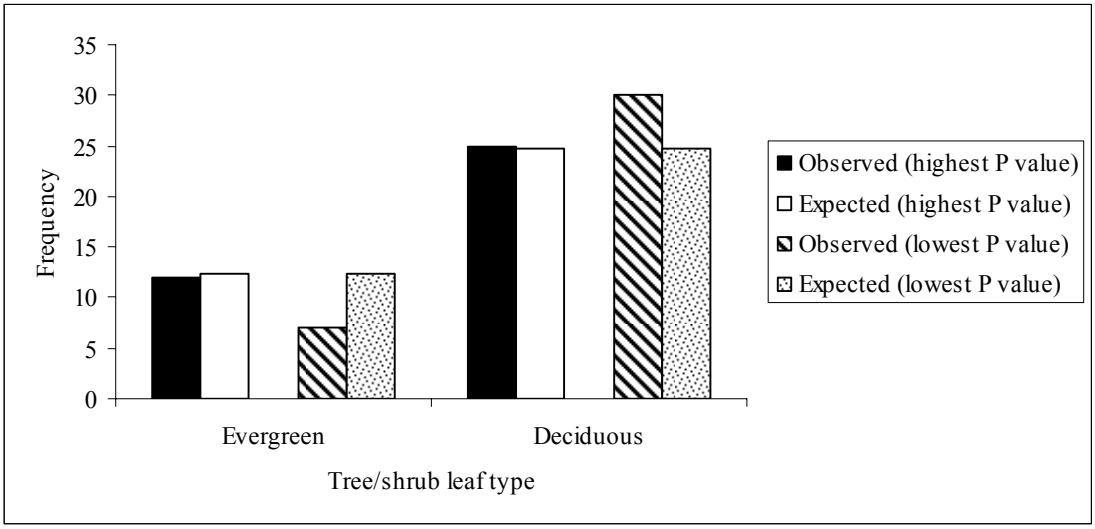
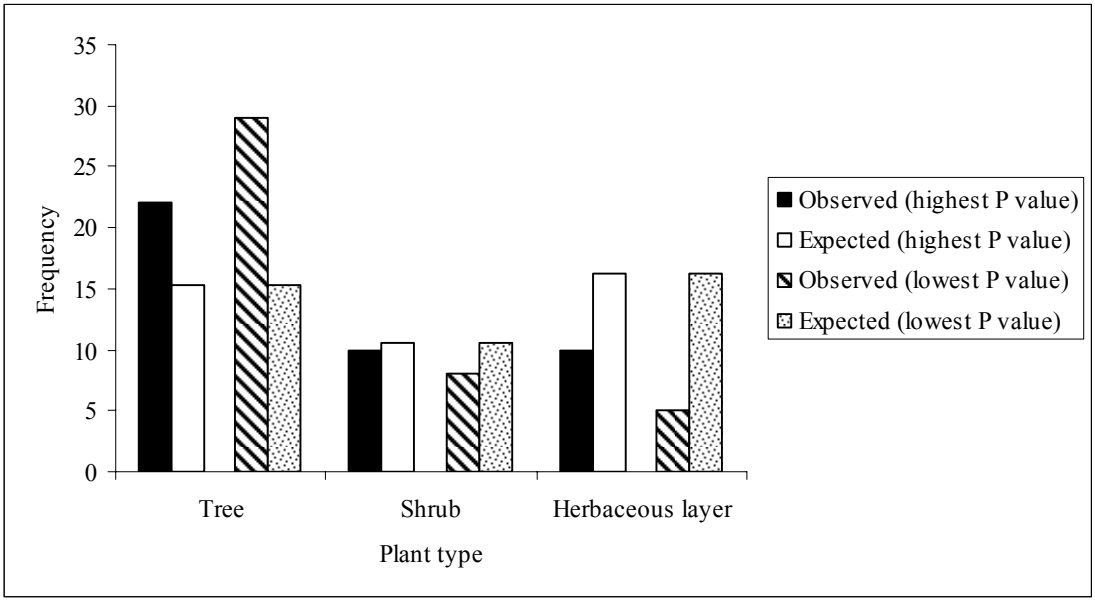


Figure 3.24 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing great tit foraging use of different plant types (trees, shrubs or herbaceous layers). The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.20d for the significance level of these P values.



Fgure 3.25 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing great tit foraging use of different plant types (trees or shrubs). The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 3.20e for the significance level of these P values.

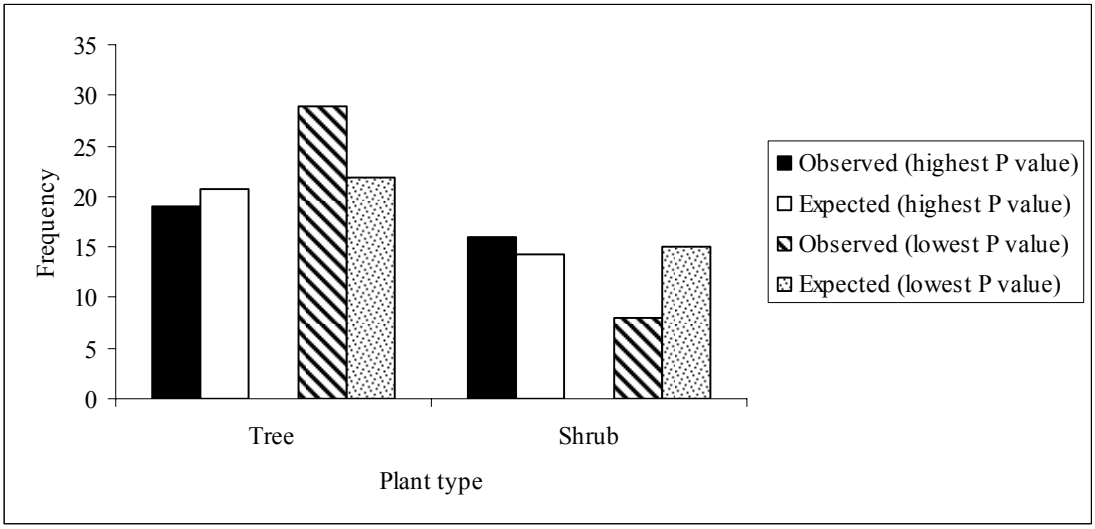


Figure 3.26 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing great tit foraging use of native (including northern and central Europe) and non-native (Americas, Asia, Med/south Europe and 'Other') trees in three different breeding periods (period one = nesting/egg laying/incubation, period two = chick feeding and period three = fledging). The figure shows the results of the highest and lowest P values obtained from six repeated tests for each breeding period, with each test using an individual bird selected by a different random number. Significance levels for each P value for each of these tests are indicated by a solid line for the highest P value and a dashed line for the lowest P value. NS indicates a non-significant test result, * indicates a significant test result at $P \leq 0.05$ and ** indicates a significant test result at $P \leq 0.001$.

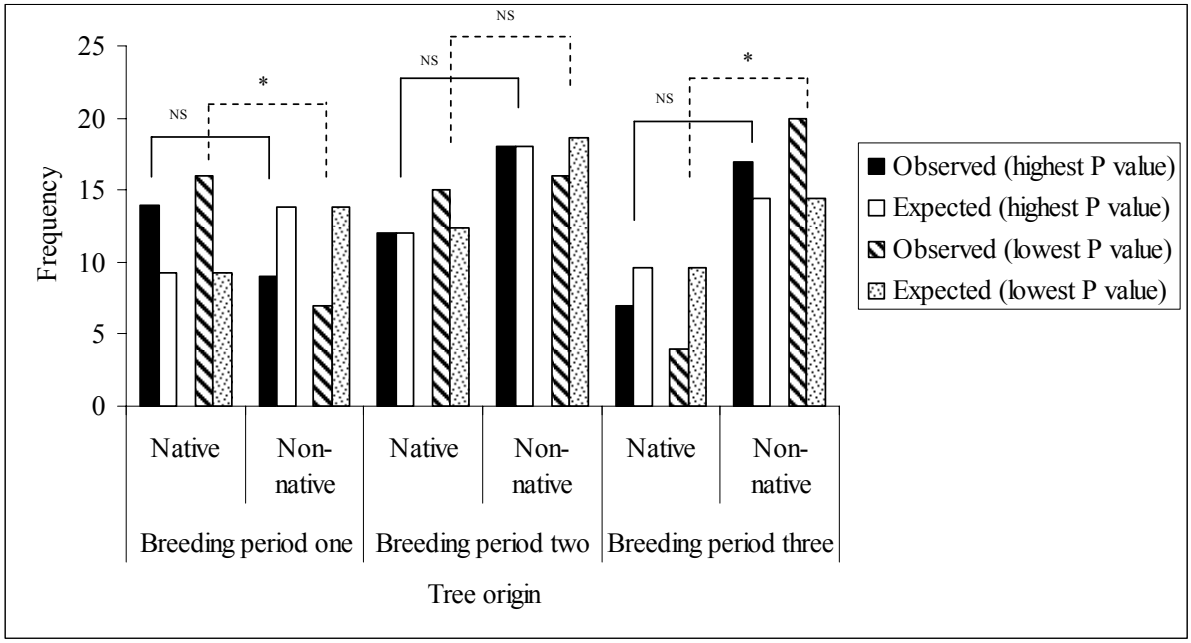
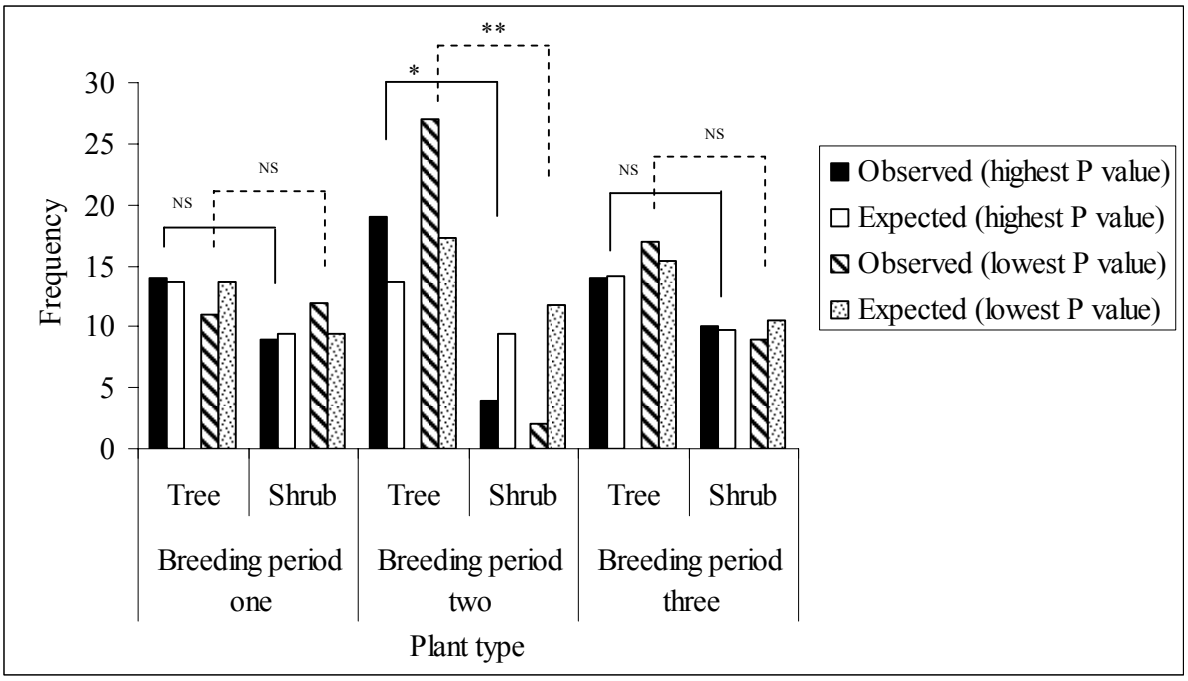


Figure 3.27 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing great tit of different plant types (trees or shrubs) in three different breeding periods (period one = nesting/egg laying/incubation, period two = chick feeding and period three = fledging). The figure shows the results of the highest and lowest P values obtained from six repeated tests for each breeding period, with each test using an individual bird selected by a different random number. Significance levels for each P value for each of these tests are indicated by a solid line for the highest P value and a dashed line for the lowest P value. NS indicates a non-significant test result, * indicates a significant test result at $P \leq 0.05$ and ** indicates a significant test result at $P \leq 0.001$.



3.4 Discussion

Blue tits and great tits have been found to differ in their foraging preferences throughout the breeding season. Overall, blue tits showed a strong preference for native plants, with trees being preferred over shrubs, and they showed a strong avoidance of evergreen trees and shrubs. Great tits however showed no strong preferences for any of the habitat types except for trees and shrubs being preferred over herbaceous layers. In their foraging in the CUBG throughout most of the breeding season they did not appear to discriminate between native versus non-native plants nor between evergreen versus deciduous plants. Although great tits did appear to prefer trees when feeding chicks in the nest, their foraging in the CUBG throughout most of the breeding season appeared to be mainly non-selective.

3.4.1 Factors affecting insect species richness and diversity: origin, plant type and leaf type

3.4.1.1 Origin of plants

Native plants have been shown to have a greater diversity and species richness of phytophagous insects than introduced plants (Brändle *et al*. 2008; Kennedy and Southwood 1984; Southwood 1961; Southwood *et al*. 1982; Southwood *et al*. 2004; Sugiura 2010; Tallamy and Shropshire 2009). Southwood (1961) and Southwood *et al.* (1982) found that introduced tree species had fewer associated insect species than the same tree species in its native country. It has been argued by the above authors that native phytophagous insects are closely adapted and specialised to the specific plants that they feed on and so are unlikely to colonise an introduced plant. This is for a number of reasons (reviewed in Brändle and Brandl 2001 and Schoonhoven *et al*.

1998); (1) insects and native plants have had more time geologically to either co-evolve with each other (co-evolutionary hypothesis) and/or the insects have had more geological time to find and colonise the plant (geological time hypothesis). Therefore the insect richness on recently introduced plants would be low. (2) Native insects are more likely to colonise an introduced plant if it is related taxonomically to a host native plant as the two plants will have similar chemical and physical traits and thus offer similar living conditions (taxonomic isolation hypothesis). Introduced plants that are not closely related to native host plants are therefore unlikely to be colonised. (3) Insect species richness increases with increasing abundance and distribution of host plants. Therefore introduced plants that have relatively low abundance will have few native phytophages feeding on them (see Southwood 1960).

3.4.1.2 Plant type

Phytophagous insects have been shown to decrease in species richness with a decrease in plant size, with a tree holding a greater species richness of insects than a shrub (Brändle and Brandl 2001; Brändle *et al.* 2008) and a shrub a greater species richness of insects than herbaceous layers (overall review in Strong *et al.* 1984).

This difference is not just interspecific. Studies have shown that insect abundance and diversity can be significantly lower in smaller trees of the same species (Campos *et al*. 2006; Jeffries *et al*. 2006) possibly due to a more complex structure in the larger trees, which may provide more niches (Brändle and Brandl 2001; Kennedy and Southwood 1984; reviewed in Southwood 1996).

3.4.1.3 Leaf type

Origin and plant type (or plant structure) have been described as the major determinants of phytophagous insect diversity (reviewed in Strong *et al*. 1984). However, leaf form - whether the plant is deciduous or evergreen - is also an important determinant (Kennedy and Southwood 1984). For example Southwood *et al.* (2004) found that the evergreen oak *Quercus ilex* had a lower phytophage biomass and lower species richness than on deciduous oaks and argued that this is to do with its 'evergreeness'. Similarly, impoverished phytophage faunas have been reported in other evergreen generas such as *Taxus* and *Ilex* (Brändle and Brandl 2001; Kennedy and Southwood 1984). Basset (1994) found evergreen leaves were less palatable to herbivorous insects than leaves of deciduous plants. Overall these studies show that phytophagous insects are found less on evergreen plants and more on deciduous plants and this is possibly due to smaller leaf sizes in evergreens (Kennedy and Southwood 1984) and/or due to higher chemical and structural defences in the slower growing evergreen leaves making the leaves much less palatable (reviewed in Basset 1994).

3.4.2 Cambridge University Botanic Garden habitat

The CUBG is dominated by exotic vegetation in an approximate ratio of 1:2 native trees and shrubs to exotic trees and shrubs and from the literature above it would appear that a greater variety and diversity of insects are to be found on native plants, and specifically, on native deciduous trees. The CUBG is also extremely heterogeneous, often a particular species is represented by only a handful of individuals whereas overall, the gardens are characterised by a great variety of genera many of which are not closely related. Consequently taxonomic isolation is probably quite high. It would therefore seem likely that the exotic plants in the CUBG have a low arthropod species

richness and abundance associated with them, and that foraging in the native plants would appear to be the best strategy.

3.4.2.1 Blue tit utilisation of habitat

Both the results from the compositional analyses and the chi-square tests confirm that blue tits have adopted this strategy by having a clear foraging preference for native trees and for native shrubs. None of the non-native categories (Asian, American, Mediterranean/southern European and 'Other') (table 3.3) were used significantly differently from each other suggesting that their origins were unimportant to the blue tits in contrast to the birds' use of native species. Blue tits were also shown to have a strong preference for trees over shrubs and for deciduous plants over evergreens and as a result are foraging in the plants that, according to the literature above should house the greatest species richness of insects. Blue tits therefore may be optimising both the quantity and quality of prey brought back to their chicks.

3.4.2.2 Differences in blue tit foraging throughout the breeding season

When the whole season was split into three different breeding periods (nest building/egg laying/incubation, chick feeding and fledging) blue tits were shown to use native trees throughout all breeding periods but used native shrubs more than expected only during nest building/egg laying/incubation. As blue tits use shrubs less than trees in the CUBG, that differences were not found between native and non-native shrubs in two of the breeding periods may have been due to a small number of observations in shrubs overall and may not necessarily reflect their true preferences. However, in section *3.4.1.2* of this discussion it was shown that insect diversity can be significantly lower in smaller trees. So the origin of a shrub may not matter so much to a blue tit

whilst chick feeding because prey may be scarce on both exotic and native shrubs. The differences between the invertebrate prey offered by native versus non-native shrubs would potentially be much smaller than those between native and non-native trees and therefore blue tits may be utilising the native trees due to their greater insect abundance compared with all shrubs.

The selection of trees over shrubs becomes less pronounced when blue tits are feeding their fledglings outside of the next box. Possibly this is as a result of the pressure of chick feeding and begging. It has for example been shown that in American dippers (*Cinclus mexicanus*) parents feed chicks more rapidly when begging is at a high intensity (Middleton *et al.* 2007). Hinsley (2000) also argued that in fragmented habitat foraging great tits facing food demands from larger broods face increased costs in terms of time and energy when travelling further distances from the chicks. They need to forage nearby to maintain both their energy levels and a steady chick feeding rate. In the CUBG the parents never seem to venture too far from the chicks on foraging bouts and families of both blue and great tits are always easy to find in the gardens due to high intensity begging (pers. obs.). If, as in American dippers, food is being delivered more rapidly to begging chicks, then parent blue tits in the CUBG may not have the opportunity to seek out the preferred native deciduous trees. Foraging may therefore be more sporadic as the parents are too pressurised to forage more effectively. Also fledglings are not as dependent on caterpillars, which predominate in the early nestling's diet (Perrins 1979) and so a wider variety of insect prey, which may be easier to find nearby, can be fed to begging fledglings. Additionally adults might also "choose" to leave fledglings in dense vegetation, which would offer some protection from predators such as jays (*Garrulus glandarius*), magpies (*Pica pica*), sparrowhawks (*Accipter nisus*) etc., all of which are found in the CUBG. This would also contribute to constraining their foraging location.

3.4.2.3 Blue tit foraging in different genera

The compositional analysis results comparing blue tit use of different genera showed that they had a clear preference for trees and shrubs of *Betula*, significantly more so than any other genus (Table 3.6), which after *Betula* (and omitting the non-genera specific habitats reported in the table) were ranked in the order *Acer*, *Populus*, *Quercus*, *Prunus*, *Sorbus* and *Fagus*. Peck (1989) similarly found that blue tits had a preference for birch (*Betula*) along with oak (*Quercus*) and sycamore (*Acer*), which was the most favoured, but an avoidance of beech (*Fagus*). Peck (1989) argued that these preferences reflected food availability, with sycamores having a high abundance of aphids but with beeches having the lowest biomass of insects of all the tree species in the study. Hypersensitivity (resistance of plants against pathogens) in *Fagus sylvatica* has been shown to reduce attacks by herbivorous galling insects (Fernandes *et al*. 2003) suggesting that it may be insect poor due to efficient plant defences. This would be consistent with its avoidance by blue tits in the CUBG.

However it is surprising that blue tits in the CUBG use *Acer* as their second preferred genus and that in Peck's (1989) study sycamores were the most preferred trees. Peck's (1989) study, being conducted between March and October, may be reflective of blue tit foraging outside of the breeding season and so represents times when blue tits use *Acer* to forage for aphids outside of chick feeding. Aphids would certainly not be a very nutritious nor high quality prey for chicks during the breeding period, the optimal prey as previously mentioned being caterpillars (Perrins 1979). In fact Kennedy and Southwood (1984) show that sycamores have only 43 species of phytophagous insects associated with them, compared with 334 on birches and 423 on deciduous oaks. As abundance of insects has been shown to increase with increasing species richness (Southwood *et al.* 1982) this would indicate a low insect abundance on sycamores.

Also, Gibb (1954) showed that only 5-9% of blue tits were found foraging on sycamores in deciduous woodland during April and May compared with 20-29% being found on oaks in April and 30%+ in May. *Acer* used by blue tits during the breeding season therefore may reflect poor insect abundance elsewhere in the CUBG possibly forcing them to forage on aphids, which would be nutritionally poor food for their chicks (Cowie and Hinsley 1988).

Also surprising is that *Quercus* was ranked behind *Betula*, *Acer* and *Populus* plants considering blue tits have often been described as oak specialists, especially during the breeding season (reviewed in Perrins 1979). This is due to the availability of a large abundance of caterpillar larvae at the time of chick feeding in early spring (Feeny 1970). In deciduous woodland during early spring, oaks have been shown to support an abundance of species-rich caterpillars due to fresh leaves being softer, having low tannin production and hence being more palatable (Feeny 1970; Murakami *et al*. 2005; Niemelä *et al*. 1982). This is in contrast to most other deciduous tree species including *Betula* and *Populus*, which were ranked before *Quercus* in this study but which have their caterpillar peak in late summer/autumn (Niemelä *et al*. 1982). In the same study, *Prunus* (ranked after *Quercus* in this study), was the only other genus to also have an early spring peak of caterpillar larvae. Blue tits would therefore be expected to have used *Quercus* and *Prunus* in the CUBG more than any other genera. That they did not may indicate poor insect abundance on these plants, which may be related to isolation of these specific genera within the CUBG. Southwood *et al.* 1982 argue that one factor influencing an insect's ability to colonise a tree is its ability to encounter a suitable habitat. In the CUBG therefore an insect's ability to find *Quercus* and *Prunus* plants would be less if individual plants are isolated, which, especially in the case of *Quercus* trees, many are. Insect abundance in *Quercus* trees can also be negatively affected by being in a mixed plot with certain other tree species (Moore and Francis 1991). *Quercus*

plants in the CUBG were mixed in with a wide variety of other plant species and so some patches may have been more insect poor depending on the neighbouring plants.

With *Betula* being ranked as most preferred it would have been interesting to have been able to split blue tit foraging in genera by breeding period to see if it held true over the whole season. Sample sizes however were too small to do this. Gibb (1954) showed blue tits increased their feeding in birch with up to 20-29% birds being recorded on birch catkins during March and April. However, he found no birds during May, when they would have been feeding their chicks suggesting that birches were not an important foraging location during chick feeding. This also fits with the finding that caterpillar larvae peaking during late summer/early autumn in *Betula* (Niemelä *et al*. 1982) would be too late for chick feeding. In the CUBG therefore *Betula* may have been preferred early when the birds were nest building/incubating - I certainly observed them feeding on catkins – but may not have been so important during chick feeding. Nevertheless Gibb's study was conducted in Wytham wood, which contains an abundance of oak trees. The birds in this oak woodland may have abandoned birch during chick rearing because they had a better option of good quality oak – an option probably not available in the CUBG. Further investigations therefore are needed to establish the use of *Betula* in the CUBG during different breeding periods.

The tests on whether native tree/shrub species were preferred over non-natives within the same genus only resulted in a significant preference in native over non-native *Betula*. It is of course possible that my analyses have not adequately tested the differences between native and non-native in the other genera and that *Betula* provided "a best" test of the question. In the garden, the *Betula* is distributed in one area in a corridor of > 100m, with native and exotic examples available in abundance and in close proximity. Blue tits foraging in this patch therefore had a choice of native or non-

native *Betula*. The majority of the other genera were more scattered and not in close proximity to each other, often being represented by only one or two plants in a patch. Therefore the distribution of foraging birds would be more skewed across the native and non-native plants of these genera and it's possible that preferences do exist that could not be detected in this study.

3.4.2.4 Great tit utilisation of habitat

Great tits, in contrast to blue tits, had no strong preference for native plants, for trees over shrubs or for deciduous over evergreen plants. Native and non-native shrubs were used non-selectively within the garden, but they did have a slight tendency to use native trees (Figure 3.21) more than non-native trees, although not significantly so. That they did not differ in their use of trees and shrubs has been shown in some other studies e.g. Gibb (1954). In this work, over the course of a year, 43% of their feeding was in trees and 53% in shrubs and may reflect differing foraging strategies/niches between blue tits and great tits (e.g. Lack 1971). However, in the CUBG, they appear to be adopting a much less advantageous foraging strategy during the breeding season than blue tits in order to feed their chicks by foraging in insect poor exotic plants and not preferentially selecting native plants. This could consequently result in lower breeding success (see Chapter 4).

3.4.2.5 Differences in great tit foraging throughout the breeding season

An interesting result however that emerged when splitting the season into breeding periods is that great tits do use native trees significantly more than non-native trees during the nest building/egg laying/incubation period. This difference was not apparent for shrubs, so only tree origin appears to be important during this period. Interestingly

this pattern was reversed during the fledging period with the non-native trees being used more than expected. Presumably this change in the fledgling period could be analogous to the situation in blue tits where their preference for trees becomes less pronounced and (as argued above) could be related to pressure from begging chicks. Great tits have been shown to have clear preferences for specific trees. For example Peck (1989) found they had a strong preference for oaks, sycamores, birches, alder and rowan; this study was conducted from March through to October and was therefore not specifically targeted at foraging during the breeding season. However, having found that great tits have a preference for native trees during the nesting building/egg laying/incubation period in the CUBG may highlight, as in Peck's (1989) study, that they have a preference for more specific plants in periods where they are not constrained by feeding their chicks. Chick feeding places high energetic demands on parent birds (Stauss *et al*. 2005; Hinsley *et al*. 2008, 2009) and demanding chicks can result in less preferred, but more available, foods being delivered to them (Cowie and Hinsley 1988). Great tits are larger birds than blue tits and so their energy needs and their offspring's energy needs would be greater. Great tits therefore may 'prefer' to forage in native deciduous trees in the CUBG but are unable to do so due to high demand for food from their offspring (Hinsley 2000) and so end up searching sporadically in nearby plants, which may not necessarily lead to successful prey capture.

In the chick feeding period, great tits made a switch to using trees preferentially over shrubs in contrast to using shrubs and trees more or less equally as during nest building/egg laying/ incubation and fledging periods. In section *3.4.1.2* of this discussion it was shown that insect diversity can be significantly greater in trees than in shrubs. Therefore, although not using deciduous or native trees preferentially as in blue tits, the fact that they are using trees preferentially over shrubs whilst feeding their chicks may be advantageous to their foraging success. Trees may potentially hold

greater numbers of prey items for their chicks, regardless of tree origin, and therefore trees become a more important foraging source, especially for young nestlings, than at other periods of the breeding season. That great tits shift to trees in the chick feeding period is also in agreement with other studies where great tits are shown to move from ground/shrub feeding to the trees in April (reviewed in Perrins 1979). In the CUBG therefore their use of trees may be as a result of an evolutionary adaptation to the large abundance of caterpillars found in the trees of deciduous woodland – of which oak woodland has been described as optimal tit habitat (Perrins 1979) - in early spring.

That great tits are mainly foraging non-selectively may indicate that they are searching in all plant types and does not necessarily indicate their success at finding prey. Naef-Daenzer and Keller (1999) found that search times were 40% greater when prey caterpillar biomass was below 20mg and argued that prey need to be a certain size for blue tits and great tits to deliver food to the nest at an efficient rate. Increasing search effort when prey is small increases the costs to the parent of satisfying their broods hunger.

3.4.2.6 Similarities in blue tit and great tit foraging

Blue tits and great tits were similar in their use of the herbaceous layer. It was used but much less than would be expected according to its availability, and used less than either trees or shrubs. Therefore it appears not to be as an important foraging resource during the breeding season, which is also supported by Gibb (1954). The herbaceous layer in the CUBG is mainly made up of cow parsley (*Anthriscus sylvestris*), which is known to house a number of aphid and moth species (Fitter and Peat 1994). Caterpillar larvae from the moths may be a good source of food for the tit chicks, but herbaceous layers having much less foliage than a tree or shrub may not hold as great an abundance of

caterpillars (see review in Strong *et al*. 1984; Tallamy and Shropshire 2009) and tits may only have turned to herbaceous layers when prey became depleted in more preferred habitats. Also, the majority of moth larvae that feed on cow parsley (one species in the family Epermeniidae and the rest in Oecoporidae, Fitter and Peat 1994) start to emerge at the beginning of May and some species only begin emerging in June and late summer (Kimber 2010). Caterpillar peak abundance would therefore be low when the chicks hatch, creating a mismatch of food supply. Blondel *et al.* (1992) found that in a deciduous oak habitat blue tits coincide hatching dates with caterpillar prey; caterpillars began emerging in early to mid April and reached their peak abundance at the start of May, just as the blue tit chicks were hatching. Tit breeding strategy has evolved to use this peak abundance of tree-dwelling caterpillars and so, in terms of first broods, they will be "mis-timed" with respect to any other caterpillars (or any other food supply) which doesn't coincide with tree-caterpillar timing (S. Hinsley, pers. comm.). Thus caterpillars on herbaceous layers in the CUBG would not be available for the chicks at their critical feeding time.

3.4.3 Blue tit and great tit foraging in urban environments

Does use of native deciduous trees in the CUBG throughout the breeding season really confer an advantage to blue tits over great tits? Native trees and shrubs in the CUBG are less abundant than non-natives by a ratio of approximately 1:2. Blue tits may have longer search times as a consequence of seeking the scarcer native deciduous trees and therefore decreased delivery rates to the chicks. In contrast, great tits, if they are foraging randomly, may have shorter search times and consequently increased delivery rates. This may result in the blue tits bringing back better quality, but lower numbers, of prey and great tits bringing back greater numbers of poorer quality prey. Both strategies represent a trade off between prey quality and search times/delivery rates but both may

result in the same output in terms of overall chick survival. Examining their breeding success is the focus of the next chapter.

Also, although native trees have been argued to be more insect diverse does this really apply in the CUBG? As previously reported, the greater the abundance of trees in an area the greater the species richness found on a particular species of tree (Kelly and Southwood 1999; Kennedy and Southwood 1984; Southwood 1961; Southwood *et al*. 1982). These studies compared the abundance of trees and associated insect diversity at the level of a country and so when the author(s) talked about the abundance of trees in an 'area' their definition of an 'area' means a country. Could this very broad hypothesis apply to fragmented habitats such as parks and gardens where single species tree abundance would be much lower? Would the insect diversity in turn be much lower even in native species? An insect's ability to find the specific species of plant (or a close taxonomic relative), which may only be represented by a few isolated plants in such a heterogeneous landscape could be severely inhibited. Smith *et al.* (2006) found that in domestic gardens abundance of trees was positively associated with species richness of insects suggesting small and fragmented patches of trees and shrubs, such as the CUBG, would be insect poor. Similarly Southwood (1957) reports a case where juniper became much rarer in southern England and as a consequence an associated insect species became extinct. In such a heterogeneous environment as the CUBG the numbers and species richness of insects would vary vastly from plant species to plant species (see Southwood 1961 for differing insect richness on different tree species) and such a varied mix of plants would also have a complete mix of phenologies (leaf emergence, budburst etc) which would in turn affect insect emergence phenology (Watt and McFarlane 1991; Feeny 1970). Consequently insect prey availability would be sporadically mixed in time and space in the CUBG making it difficult for any forager.

3.4.4 Further investigations

Understanding the impact of exotic flora on the species richness of insects is of importance and interesting in its own right, including the influence that phenology may have. It is critical in understanding how urban landscapes affect predatory species such as tits, as this is an indication of ecosystem function. It is hoped that future work in the CUBG will include sampling of the invertebrate fauna, which is unfortunately beyond the scope of this PhD. Current work in the CUBG involves collection of the faecal sacs produced by the chicks and filming at and in nest boxes. Collection of the faecal sacs have so far produced only small sample sizes and camera boxes, that were introduced in the breeding season of 2009, were not taken up. Recent adjustments to the nest boxes to encourage bird use and a more intensive collection of faecal sacs on a number of days throughout the chick feeding period should correct the outlined problems and offer insights into the type and abundance of prey that is being fed to the young in the nest boxes.

3.4.5 Conclusions

To summarise, I argue that blue tits, by using native deciduous trees preferentially, have a more advantageous foraging strategy throughout the breeding season than do great tits, which appear to lack a well-defined preference for vegetation characteristics when foraging. However, in urban environments, insect abundance and species richness may be much lower than in woodland due to lower plant abundance, a high ratio of exotic plants to natives and high plant heterogeneity. Also availability and isolation of usually preferred genera such as *Quercus* may have forced blue tits to switch to less-nutrient rich, but more abundant, prey for their chicks found in different genera. Both blue tit and great tit foraging success therefore may be poor when compared with other habitat

types such as woodland and those with native scrub and as a consequence could negatively affect their breeding success. The effects of habitat type on breeding success will be the subject of the next chapter.

CHAPTER 4

Reproductive success of blue tits and great tits in relation to habitat quality

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4.1 Introduction

Avian habitat quality is a good predictor of reproductive performance. A variety of factors have been treated as indicative of habitat quality: vegetation structure (Sherry and Holmes 1985) and fragmentation (Hinsley *et al*. 2002, 2009), climate (Hinsley *et al*. 2006), vegetation characteristics such as age of tree stand (Burton 2009; Nikolov 2009) and invertebrate availability (Alatalo *et al*. 1985; Cummins and O'Halloran 2002; Peach *et al*. 2004). Specific species often have an affinity with specific habitat types. Blue tits (*Cyanistes caeruleus*) for example have an affinity with oak woodland (Perrins 1979) and good reproductive performance has been found to be associated with relative abundance or proximity of oak trees (Hinsley *et al.* 2009; Stauss *et al*. 2005). For blue tits in oak woodland, the interplay of some of these habitat factors, namely vegetation structure (oak canopy), vegetation characteristics (mature oak) and invertebrate availability (a peak abundance of caterpillar prey during the breeding season (Perrins 1979, 1991; Tremblay *et al.* 2003, 2005)) work to create high quality habitat. However, factors such as habitat loss and fragmentation can have a negative impact on habitat quality.

Habitat loss and fragmentation has become of increasing concern to conservation biologists, being recognised as an important cause of species declines worldwide (Sih *et al*. 2000). Some work has begun to address the question of how habitat fragmentation affects habitat quality and how habitat quality in turn affects breeding success in birds

(Cowie and Hinsley 1988; Hinsley *et al.* 1999). In highly fragmented woodland, for example, both blue tits and great tits (*Parus major*) have been shown to have lower breeding success in smaller woodland fragments (Hinsley *et al.* 1999; Loman 2003), which is probably due in part to a low abundance of prey. This has also been found in other species including the robin (*Erithacus rubecula*), long-tailed tit (*Aegithalos caudatus*) and marsh tit (*Poecile palustris*) (Hinsley *et al.* 1996) so the issue is not just species specific. Similarly Tremblay *et al.* (2005) found that blue tits in 'poor' habitat in Corsica had to work harder by increasing foraging effort in order to maintain similar levels of caterpillar delivery to chicks as in the 'rich' habitat. Some North American studies on migratory neotropical birds have also addressed the deleterious effects of habitat fragmentation on birds by looking at woodland size. These studies have found smaller woodland fragments to have reduced prey biomass and abundance than larger woods (Burke and Nol 1998) and have argued that increased brood parasitism and nest predation may be associated with the higher proportion of forest edges in smaller fragments (Wenny *et al*. 1993).

However, in the increasingly populated modern landscapes of Britain and Europe, some researchers have recognised the growing importance of studying breeding performance of birds outside of their usual habitats (Dhondt *et al*. 1984; Hinsley *et al*. 2008, 2009; Loman 2003; Peach *et al*. 2008). Blue tits and great tits for example, although being described as a woodland species, are now increasingly found breeding in urban habitats, where habitat patches are likely to be small. That they are able to occupy different habitats other than woodland, unlike some specialist woodland birds (Hewson *et al*. 2007) could be argued as favourable to these generalists. Conversely, this may be at the expense of poorer breeding performance. For example, a study comparing the energetic costs of blue tits and great tits living in urban parkland to those in woodland has shown that parent birds work about 64% harder than in a wood to raise each chick as the result

of the increased numbers of gaps in the habitat combined with smaller brood sizes (Hinsley *et al*. 2008). Gaps may be physical gaps, open areas between trees, or may be 'functional gaps', where trees and shrubs are present, but are not suitable habitat.

These 'functional gaps' are often due to an abundance of exotic plant species, common now in parks and gardens, which often support low abundances of insectivorous bird food (Burghardt *et al.* 2008; Southwood *et al*. 1982; reviewed in Tallamy 2004; Tallamy and Shropshire 2009) and consequently cause difficulties for foraging birds. In fact non-natives that are predicted to be unpalatable to herbivorous insects may be favoured in residential gardens over insect-palatable natives (Tallamy 2004), thus intensifying the problem. Additionally, exotic plants may flower and leaf at different times to natives, and with herbivorous insects often being closely synchronised to budburst (Buse and Good 1996), this could create a mismatch between the timing of bird breeding and the peak abundance of invertebrate chick prey. Temperature may also play a part: species of the same plant have been shown to bud earlier in warmer temperatures (Doi and Katano 2008), so in urban environments where temperature is often higher (Voogt 2002) all plants, irrelevant of origin, may bud earlier, again creating disparities between chick demand for food and food availability. These disparities may also be evident as a consequence of the increased availability of bird-feeder food in parks and gardens. For example Schoech and Bowman (2001) found that suburban Florida scrub jays (*Aphelocoma coerulescens*) with access to anthropogenic food were able to breed earlier but bred too early in relation to the availability of the arthropod food needed to feed their young. Female birds may therefore be able to achieve breeding condition sooner by feeding on anthropogenic food but consequently this may affect their perception of food availability.

In this study, the consequences of habitat fragmentation for blue tits and great tits, two generalist bird species that mainly feed their young on tree dwelling caterpillars (Perrins 1991), are explored by comparing their breeding success in urban parkland (with an abundance of exotic flora) to other marginal habitats (with native flora) and to small and large woodlands. Mature oak woodland has been described as the optimal habitat for blue tits and great tits as oaks offer an abundance of caterpillar prey for foraging parents throughout the breeding season (Kluijver 1951; Lack 1955, 1958; Perrins 1965, 1979, 1991). I therefore hypothesise that the large woods, which contain oak as one of the dominant species, will have the best breeding success, and urban parkland, which has low numbers of oak trees, a high abundance of exotic vegetation and high levels of fragmentation, the poorest.

In addition, the characteristics within urban parkland are investigated to assess the effects of 'functional' and 'structural' habitat gaps (Hinsley *et al*. 2008) on breeding success in blue tits and great tits. Functional gaps are explored by examining the genera, leaf type (deciduous or evergreen) and origin of the flora available within the urban park. Structural gaps are explored by examining physical spaces in the vegetation. Understanding the characteristics of urban parkland that can reduce its quality as habitat for certain breeding bird species is very important to assess the consequences that the rapidly changing landscape may have for their future survival.

4.2 Methods

4.2.1 Site descriptions

Reproductive performance of great tits and blue tits was measured for pairs breeding in nest boxes in large woods, small woods, marginal scrubby habitats and urban parkland.

Large and small wood data were provided by S. Hinsley. Large woods comprised Brampton Wood (Wildlife Trust woodland, 52° 19' N, 0° 16' W, 132 ha, 22 boxes) and Wennington Wood (privately owned, 52° 24' N, 0° 10' W, 72 ha, 36 boxes) (blue tit data only) in Cambridgeshire and up to 36 small woods (0.1-1.39 ha) with up to a total of 56 boxes were located in Cambridgeshire and south Lincolnshire. See Hinsley *et al.* (2009) for descriptions of Brampton Wood and the small woods and Hill *et al.* (2004) for a description of Wennington Wood, but essentially they are all mixed deciduous, the canopy dominated by oak, ash and field maple and the understory by hawthorn, blackthorn and hazel.

Marginal scrubby habitats included the area of St Edmund's Fen on Wicken Fen (52° 18' N, 0° 17' E, 55 boxes, St Edmund's Fen ~17 ha) and Cow Lane (52° 20' N, 0° 09' W, 60 boxes of which 16 were accessible to blue tits only, ~ 77 ha) both in Cambridgeshire. Cow Lane, data having been provided by N. Harrison, is a private nature reserve, established by Lafarge, based in an old gravel pit site. The nest boxes are located in various sites within Cow Lane: 'osier stand' (~11.8 ha), at the centre of which is an excavated pool (dominated by willow scrub), 'hedgerows' (varying in number and species of trees, with a few old oaks but dominated by hawthorn and willow scrub) and 'fisheries' (with woodland-like canopy structure and diverse trees and shrubs). At Wicken Fen, the area of St Edmund's Fen (see Figure 4.1) is covered by woody shrubby vegetation known as 'carr' (Friday *et al*. 1997). Tall trees are limited in distribution and the carr makes up a dense thicket of fairly impenetrable scrub. Pathways are kept clear by National Trust staff members to allow access to the nest boxes, which are positioned in near proximity to the edges of the pathways. Willows are the predominant flora, interspersed with hawthorn, buckthorn and bramble. Mature trees, when present include poplars and oaks. Reeds are also present in more open and boggy areas such as pathways.

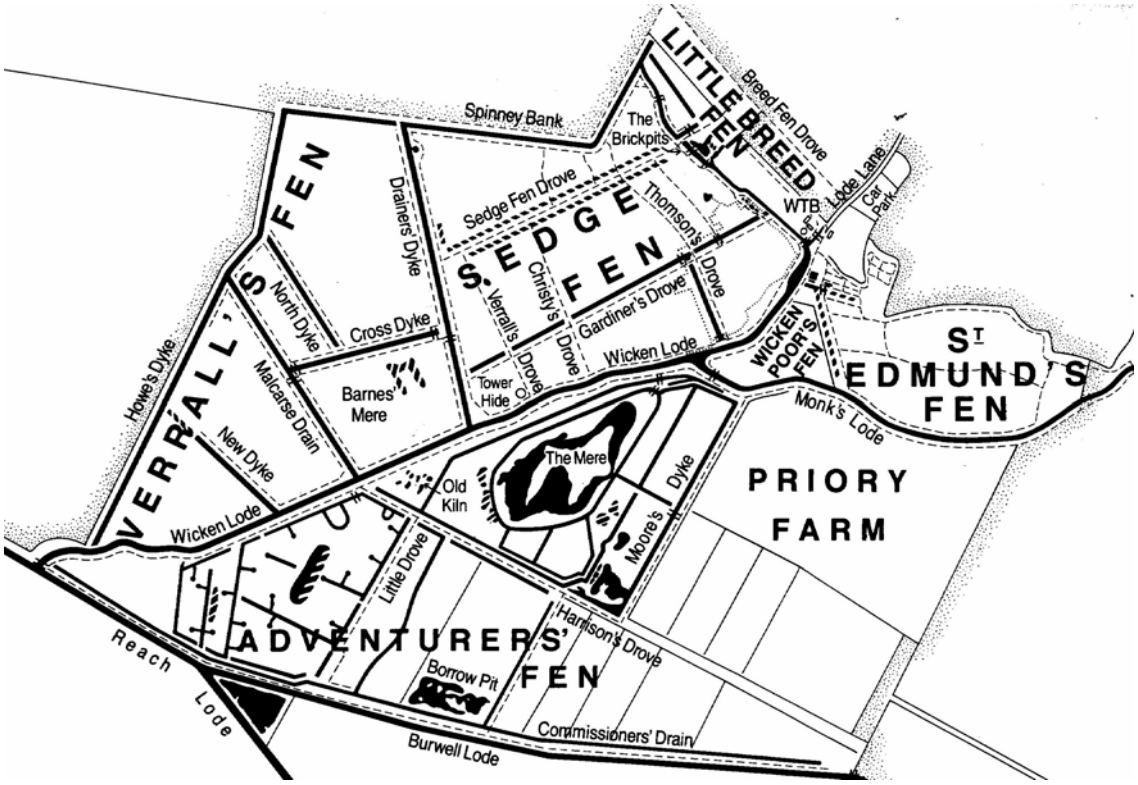


Figure 4.1 Map of Wicken Fen from Friday and Harley (2000).

Urban parkland was represented by the Cambridge University Botanic Gardens (CUBG) (52° 12’ N, 0° 08’ E, 42 boxes, ~16.5 ha) (see Chapter 2 for a detailed description).

At Wicken Fen and the CUBG several of the boxes were designed with a hole that would allow only blue tits (approx 25mm) and not great tits to enter (22 at CUBG and 20 at Wicken Fen). The remaining boxes were accessible to both species (approx 28mm). This was to ensure more or less equal uptake of boxes by both species since blue tits can be out-competed by great tits for box occupancy.

4.2.2 Bird breeding performance

In order to determine first egg date and clutch size, inspection of boxes was carried out beginning on approximately April 1st and continuing at no less than weekly intervals. First egg date is the date on which the first egg of a clutch is laid by a female and assumes that she lays one egg (usually around 6am) per day until the clutch is completed (Perrins 1979). Clutch size refers to the total number of eggs that an individual female lays in one breeding attempt. When a female lays the final or the final but one egg of a clutch she will begin incubating them (although earlier incubation is possible in late nesters, Perrins 1979). Therefore if she was found to be incubating when the box was checked the observer would replace the box lid, wait for her to exit and then count the clutch. The female was not handled during incubation; this acts to minimise stress to the bird and to reduce the risk of desertion (Hinsley *et al*. 1999).

High weasel (*Mustela erminea*) predation rates at Wicken Fen and to a lesser extent at Cow Lane often resulted in a number of second breeding attempts being made. Second breeding attempts would potentially bias the results of any analyses and so needed to be excluded, but often it was unclear which were first or second attempts at these sites. Therefore the average and standard deviation of first egg dates within a year were calculated and any egg dates one standard deviation from the mean were excluded from the analyses along with any associated data on that particular breeding attempt (e.g. clutch size, weights etc). At Wicken Fen, where weasel predation was especially high, the egg dates were also plotted on a histogram to examine the shape of the data and look for potential cut off points between first and second attempts. A conservative estimate combining the results from the average and standard deviation calculations and the cut off from the histogram was then used to determine the breeding attempts that were to be excluded.

Hatching date was estimated as 14 days after the female began incubating (including the day that the last egg of the clutch was laid). At the CUBG and Wicken Fen the nest was checked for hatching at least 2 days prior to the estimated hatching date and every day hence until hatch date was established. At Cow Lane nests were checked one day prior to hatching and if this wasn't possible, on hatching day itself. If chicks were found to be already hatched on the calculated hatching day, the chicks were assessed by sight (only by experienced observers) to decide their age. If the female was found to be on the nest, the observer would replace the lid and only look for hatching once she had exited the box.

On their 11th day (counting the day that they hatched as day 0) nestlings were counted and ringed with a uniquely numbered British Trust for Ornithology (BTO) aluminium ring and weighed, (using a Pesola or Salter spring balance to the nearest 0.1g). Very small chicks (runts) were not ringed if their legs were deemed too undeveloped to prevent the ring slipping over the toes and it was assumed that they would die before fledging. The mean chick weight (excluding runts) and total biomass (including runts) in each box was calculated. Since day 11 chicks were so small at the CUBG, making runts difficult to determine by eye, frequency tables were generated with 5% values calculated using all individual chick weights from all boxes for each species. Any weights below 5 % were deemed to be runts and were excluded from the mean brood weight calculations.

No visits were made following ringing on the 11th day until after the chicks should have fledged (19-20 days after hatching) to avoid risk of the nestlings leaving the nest prematurely. When the boxes were visited, the number fledged was determined by counting any remains (including rings) and subtracting this from the total nestlings that

were ringed on day 11. Fledging success was determined as the number fledged expressed as a proportion of clutch size.

Nest failures and possible causes were noted and if nests were found to have been predated the nest material was removed on discovery since the box had potential to be re-occupied. For Wicken Fen and Cow Lane the number of chicks fledging, i.e. 0, was not included in analysis for nests that had failed due to known predation as this would have led to a biased outcome, testing for predation effect rather than the effect of habitat on food availability. Similarly, the number of chicks fledging from nests that had been abandoned (cold, un-hatched eggs presumed due to the death/desertion of the female), would also have generated zero values not necessarily related to food availability for chicks, and thus were not included for Cow Lane, Wicken Fen and the CUBG. At the CUBG however, if a whole nest had failed due to starvation before the chicks were ringed on day eleven these were included as zeros in the number of chicks fledging variable. As colour ringed birds were followed daily and it was known which nest box they were associated with it was usually known if the chicks had starved; the birds would no longer be seen entering and leaving the nest box. The nest box was also checked to confirm the presence of dead chicks. For woodland data only "live" nests were included at each stage of breeding, zero values were not included.

Results for both species were examined for seven years for large and small woods, the CUBG and for great tits at Cow Lane (2003-2009), for nine years for blue tits at Cow Lane (2000-2009) and for two years at Wicken Fen for both species (2007-2008). Breeding success was measured at Wicken Fen during 2006 but due to very heavy weasel predation all 2006 data were excluded from the analyses. Small woods were combined into one 'small wood' category for analyses. In total, data were available for 22 small woods for blue tits and 31 for great tits.

4.2.3 Statistical analysis

All statistics were carried out using the SPSS 16.0 for Windows package (2007).

4.2.3.1 Reproductive success in different habitats

To test for differences in breeding success of blue tits and great tits in the different sites, type III General Linear Models (GLM) were used to analyse the following response variables: first egg date, mean mass of chicks and biomass of chicks at 11 days of age.

Type III Generalised Linear Models using a Poisson regression with a log link function were used to analyse the following response variables: clutch size and number of chicks fledged. These variables are count data, and Poisson distributions are thus appropriate. To estimate the scale parameter, which is usually assumed to be one, I used the Pearson chi-square method as suggested by McCullagh and Nelder (1989) for Poisson distributions. This method generates more conservative variance estimates and significance levels. I tested for over dispersion (greater variability than expected) in the Poisson models by examining the values for deviance and Pearson chi-square test, which should be near to one if the model is not over dispersed. Further checks were made by constructing a likelihood-ratio test comparing the Poisson and negative binomial regression models. If the value for the likelihood ratio was larger for the Poisson regression than the negative binomial then over dispersion was not likely. None of the models showed over dispersion.

To test the fledging success of chicks across the different sites type III Generalised Linear Models with binomial distribution and logit link were used with number of chicks fledged as the response variable and clutch size as the trials variable (or binomial

denominator). The scale parameter was fixed at one. Binomial models essentially test the number of 'successes' from a given number of trials and so this is akin to calculating a percentage of the number of eggs producing fledglings.

Fixed variables for all types of model were year and site and year x site interaction. Interactions were used to test for any differences at individual sites between years. Egg date was used as a covariate when testing clutch size. Egg date and clutch size and egg date x clutch size interactions were used as covariates when testing mean weight, biomass, number fledged and fledging success. Any insignificant variables, unless the variable was approaching significance ($P < 0.10$) were removed from the model and the resulting model was reported. If an interaction term was significant the variables within the interaction were retained separately in the model irrespective of their significance.

For all reported models, the three assumptions of normality, homogeneity and linearity were checked by plotting a histogram of the residuals for normality, a scatterplot of the residuals against the predicted values for homogeneity and a scatterplot of the residuals against any covariates (as described in Hawkins 2009 and Grafen and Hails 2002). All models fitted the assumptions of GLM except for biomass as a response variable, which showed a number of outliers on the scatterplot of residuals against the covariate clutch size for both blue and great tits, creating a slight skew in the histograms. Looking at the plots, the vast majority of outliers fell outside of two standard deviations (SD) from the mean of the residuals and so any outside of this two SD margin were removed from the analysis. Looking at the data it would appear that the outliers were the result of extreme brood reduction. In total, these checks resulted in data for 13 nest boxes for blue tits (1 at the CUBG, 2 at Cow Lane, 2 at Brampton Wood, 2 at Wennington Wood and 6 in small woods) and 14 nest boxes for great tits (2 at the CUBG, 1 at Cow Lane, 5 at

Brampton Wood and 6 in small woods) being removed. Once the outliers were removed the models for biomass for blue and great tits now fitted the GLM assumptions.

4.2.3.2 Habitat and reproductive success within the CUBG

To test for differences between the fledging success of blue tits and great tits at the CUBG a type III Generalized Linear Model was used (a binomial regression model) with a logit link. The number of chicks fledged was the response variable and clutch size the trials variable (or binomial denominator). Fixed variables were year and species.

The influence of different habitat variables (habitat type) on breeding success within the CUBG was tested using mixed models. Habitat variables comprised percentage data calculated from a 100m radius buffer and a 25m radius buffer around an individual nest box (see Chapter 3 methods section *3.2.4.1* for detailed description) and included: 1) % of native trees and shrubs, 2) % of non-native trees and shrubs, 3) % of deciduous trees and shrubs, 4) % of evergreen trees and shrubs, 5) % of gaps (defined as the absence of any trees, shrubs, herbaceous layers, planted beds or hedges), 6) % of *Quercus* trees and shrubs (including native and non-native and evergreen and deciduous plants), 7) % of *Betula* trees and shrubs (including native and non-native plants, all were deciduous) and 8) % *Acer* trees and shrubs (including native and non-native plants, all were deciduous). Thirteen boxes for the 25m habitat and twelve for the 100m habitat for blue tits and twelve boxes for both 100m and 25m habitat for great tits were used in the analyses.

In the mixed model, clutch size, mean weight, biomass and number fledged were used as response variables with habitat type, year and year x habitat type interactions as categorical explanatory variables. As habitat was calculated around nest boxes, an

overrepresentation of an individual box could bias the results by increasing the replicates of available habitat around an individual box. Therefore nest box was used as a random effect to control for any pseudo-replication of boxes across years. In the final reported model habitat type was always retained whether it was significant or non-significant as it was the variable of most interest. If habitat type was close to significance and the other explanatory variables were not, then they were removed in turn to assess the effects on the significance of habitat type and, based on the outcome, a particular model was then chosen to report. As described above, for all reported models, the three assumptions of normality, homogeneity and linearity were checked. The models were fitted by the method of restricted maximum likelihood (REML).

4.3 Results

4.3.1 Reproductive success in different habitats

The models outlining the effect of habitat type on various reproductive parameters are summarised in Tables 4.1 (for tests using General Linear Models), 4.2 (for tests using Generalised Linear Models with Poisson distribution) and 4.3 (for tests using Generalised Linear Models with binomial distribution) and show that reproductive performance differed significantly between the sites. Overall, reproductive success for both blue tits and great tits was lower in the CUBG than in large woods and was lower than or similar to marginal sites (Cow Lane, Wicken Fen and small woods). The species also differed in their reproductive performance and the results of these site and species differences are outlined below and in Tables 4.4 to 4.9.

4.3.1.1 First egg date and site

Blue tits had significantly later egg dates in the CUBG than in both large wood sites (Brampton and Wennington) and non-significantly different first egg dates in the CUBG compared to Cow Lane and small woods. There was a slight but non-significant trend for earlier egg dates in Wicken Fen than in the CUBG at P>0.10 (Table 4.4). Great tits laid significantly earlier in the CUBG than at Cow Lane and small woods. Wicken Fen and Brampton Wood did not differ significantly from the CUBG in first egg dates (Table 4.5).

4.3.1.2 Mean mass and site

Blue tits had significantly lighter chicks at the CUBG than at Wicken Fen (although with a sample of only 13 nests at Wicken Fen this result may not have been truly representative of the site). Mean chick mass at small woods and large woods did not differ significantly from the CUBG and there was a slight trend at the P<0.10 level for lighter chicks at Cow Lane (Table 4.4). For great tits, mean chick mass was significantly lower at the CUBG than at Brampton Wood and Wicken Fen. Mean chick mean mass did not differ significantly at Cow Lane and small woods compared to the CUBG (Table 4.5).

4.3.1.3 Biomass and site

For both species, biomass was significantly lower at the CUBG than at any other site (Tables 4.4 and 4.5).

4.3.1.4 Clutch size and site

Blue tits had significantly smaller clutches at the CUBG than in small woods and both large woods. Clutch sizes at Wicken Fen and Cow Lane did not differ significantly from the CUBG (Table 4.6). Great tits had significantly smaller clutches at the CUBG than at any other site (Table 4.7).

4.3.1.5 Number of chicks fledging and site

Great tits fledged significantly lower numbers of chicks at the CUBG than at Brampton Wood (Table 4.7) and blue tits fledged significantly lower numbers of chicks at the CUBG than at Wicken Fen (Table 4.6). The number of chicks fledging at Cow Lane and small woods did not differ significantly from those at the CUBG for both blue tits and great tits. Great tits also fledged non-significantly different numbers at the CUBG compared to Wicken Fen. There was a slight but non-significant trend for blue tits to fledge lower chick numbers at the CUBG than at Brampton Wood and Wennington Wood ($P<0.10$).

4.3.1.6 Fledging success (proportion of eggs that produced fledglings) and site

Blue tits fledged a significantly lower proportion of chicks at the CUBG than at Wicken Fen and both large woods (Brampton and Wennington). Fledging did not differ significantly when comparing CUBG with Cow Lane and small woods (Table 4.8). Great tits fledged a significantly lower proportion of chicks at the CUBG than at Wicken Fen and Brampton Wood and to a non-significant degree ($P<0.10$) also at small woods. At Cow Lane a non-significantly different proportion of chicks fledged compared to the CUBG (Table 4.9).

4.3.1.7 Other model variables

Significant differences were found between years for both species for first egg dates, mean chick mass, biomass (Table 4.1) and fledging success (Table 4.3), and for clutch size in blue tits and for number fledged in great tits (Table 4.2), indicative of 'good' and 'bad' reproductive years across all sites irrespective of habitat type. Interactions between site and year suggest that sites differ in sensitivity to environmental conditions, all sites not responding in the same way in a 'bad' year or in 'good' year.

Clutch size contributed significantly to the models for mean mass and biomass for both species (Table 4.1) and to the model for number of chicks fledged for great tits (Table 4.2). The pattern for mean mass against clutch size was not particularly strong for blue tits and differed between sites (Figure 4.2a): the CUBG, small woods and to an extent Wicken Fen (although a small sample size here makes it inconclusive) show a decrease in mean mass with increasing clutch size. Brampton Wood follows this same pattern to an extent but in general, mean mass of chicks at this site remain unaffected by clutch size. However, Cow Lane and Wennington Wood show the opposite effect, with a decrease in mean chick mass as clutch size decreases. Great tits at Cow Lane also followed this pattern (Figure 4.2b) but for all other sites for great tits mean mass of chicks decreased with increasing clutch size. For both blue tits and great tits at all sites biomass increased with increasing clutch size (Figure 4.3a and b).

First egg dates contributed significantly to the models for biomass (Table 4.1), clutch size (Table 4.2) and fledging success (Table 4.3) for both blue tits and great tits and number of chicks fledging for blue tits (Table 4.2). Both clutch size and biomass for both species and number and percentage of chicks fledging for blue tits decreased with increasing first egg date at all sites (Figure 4.4a–b, Figure 4.5a-b, Figure 4.6 and Figure

4.7a respectively). For great tits at the majority of sites, the percentage of chicks fledging also decreased with increasing first egg date, although at Wicken Fen there appeared to be no real pattern, with both late and early clutches doing well (Figure 4.7b). A small sample size however may make this unrepresentative. At the CUBG great tits had a particularly steep drop in percentage of eggs fledging with increasing egg date with later, but not particularly late clutches (up to median first egg date of 20) only fledging between 20-60% of fledglings. In contrast, at Brampton Wood, although there was a trend for earlier clutches to fledge a greater percentage, late clutches were not unsuccessful, often fledging >80% of chicks. The same was true for blue tits at Wennington Wood.

The model for biomass in great tits included an interaction term - 'clutch size x egg date'. Although not significant, this interaction term was also in the model at $P<0.10$ for number of chicks fledging for blue tits, suggesting a slight trend. This highlights differences in the effect of clutch size and egg date together on biomass in great tits (Table 4.1) and on the number of chicks fledged in blue tits (Table 4.2). An example of this interaction is shown in Figure 4.8 where having a clutch of 12 eggs early on in the season appears to be beneficial but 12 eggs later on in the season can lead to a sharp decline in the number of blue tit chicks fledging, more so in some cases than having a smaller clutch of 8.

Table 4.1 Comparison of breeding success (first egg date, mean chick mass and chick biomass) between sites (CUBG, Wicken Fen, Cow Lane, Brampton Wood, Wennington Wood (blue tit only) and small woods) using General Linear Models.

Species	Response variable	Tests of between-subjects effects (F value)						Corrected model F value	Degrees of freedom (df, error df)	Adjusted R^2	Final model equation
		Site	Year	Site x Year interaction	Egg date	Clutch size	Egg date X Clutch size interaction				
Blue tit	Egg date	7.62***	17.55***	1.78*	N/A	N/A	N/A	7.56***	40, 313	0.43	Site + Year + Site X Year
	Mean mass	16.98***	1.95*	1.49¹	†	3.52*	†	3.85***	40, 240	0.29	Site + Year + Site X Year + Clutch size
	Biomass	26.18***	4.43***	†	15.63***	75.30***	†	36.40***	16, 249	0.68	Site + Year + Egg date + Clutch size
Great tit	Egg date	27.34***	37.30***	2.98***	N/A	N/A	N/A	15.12***	30, 442	0.47	Site + Year + Site X Year
	Mean mass	26.00***	7.60***	2.53***	†	7.97**	†	7.27***	30, 352	0.33	Site + Year + Site X Year + Clutch size
	Biomass	36.65***	11.20***	†	10.19**	65.44***	13.89***	57.93***	13, 345	0.67	Site + Year + Egg date + Clutch size + Egg date X Clutch size

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, ¹ $P \leq 0.10$, † not significant so excluded from final model, N/A non applicable to the model

Table 4.2 Comparison of breeding success (clutch size and number of fledging chicks) between sites (CUBG, Wicken Fen, Cow Lane, Brampton Wood, Wennington Wood (blue tit only) and small woods) using Generalised Linear Models with Poisson regression and log link.

		Wald chi-square test of model effects						Overall model		
Species	Response variable	Site	Year	Site x Year interaction	Egg date	Clutch size	Egg date X Clutch size interaction	Chi-square a, b		Final model equation
Blue tit	Clutch size	100.78***	27.81***	†	41.50***	N/A	N/A	205.99***a	15 *df*	Site + Year + Egg date
	No. fledged	35.93***	13.54	38.40*	4.81*	0.00	2.80[1]	255.41***a	42 *df*	Site + Year + Site X Year + Egg date + Clutch size + Egg date X Clutch size
Great tit	Clutch size	115.28***	7.76	31.44*	17.26***	N/A	N/A	170.39***a	31 *df*	Site + Year + Year X Site + Egg date
	No. fledged	79.19***	20.32**	46.70**	4.06*	68.68***	†	50.65***b	1 *df*	Site + Year + Year X Site + Egg date + Clutch size

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, [1] $P \leq 0.10$, † not significant so excluded from final model, N/A non applicable to the model, a. calculated using likelihood ratio chi-square (compares intercept model against fitted model), b. calculated using Wald chi-square (intercept only model)

Table 4.3 Comparison of fledging success between sites (CUBG, Wicken Fen, Cow Lane, Brampton Wood, Wennington Wood (blue tit only) and small woods) using Generalised Linear Models with binomial regression and logit link.

Species	Response variable	Trials variable	Wald chi-square test of model effects				Omnibus test		Final model equation
			Site	Year	Site x Year interactions	Egg date	Likelihood ratio chi-square		
Blue tit	No. fledged	Clutch size	95.05***	27.31***	97.23***	24.77***	448.98***	40 *df*	Site + Year + Site X Year + Egg date
Great tit	No. fledged	Clutch size	180.97***	18.07**	89.91***	10.56***	411.87***	30 *df*	Site + Year + Site X Year + Egg date

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, ^{1} $P \leq 0.10$, † not significant so excluded from final model

Table 4.4 Parameter estimates generated by General Linear Model tests comparing blue tit first egg date, chick mean mass and chick biomass at the CUBG to Wicken Fen, Cow Lane, Brampton Wood, Wennington Wood and small woods. Note: a negative parameter estimate for egg date represents an earlier first egg date than at the CUBG and a positive parameter estimate represents a later first egg date than at the CUBG. For mean mass and biomass a negative parameter estimate represents a lighter mass than at the CUBG and a positive parameter estimate represents a heavier mass than at the CUBG.

Response variable	Site (N) by site (N)		Parameter estimate	*t* value	Standard error
Egg date	Botanic Gardens (66)	Wicken Fen (40)	-4.00	-0.80[1]	2.12
		Cow Lane (91)	0.20	0.08	2.45
		Brampton Wood (22)	-6.30	-2.02*	3.12
		Wennington Wood (59)	-5.30	-2.04*	2.60
		Small woods (76)	-1.87	-0.80	2.34
Mean mass	Botanic Gardens (55)	Wicken Fen (13)	1.55	2.62**	0.59
		Cow Lane (65)	-0.91	-1.78[1]	0.51
		Brampton Wood (18)	1.08	1.63	0.66
		Wennington Wood (58)	0.82	1.47	0.56
		Small woods (72)	-0.28	-0.55	0.50
Biomass	Botanic Gardens (54)	Wicken Fen (13)	15.29	3.31***	4.62
		Cow Lane (63)	13.63	4.41***	3.10
		Brampton Wood (17)	31.31	7.09***	4.42
		Wennington Wood (54)	32.66	10.75***	3.04
		Small woods (65)	15.33	5.14***	2.98

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, [1] $P \leq 0.10$,

Table 4.5 Parameter estimates generated by General Linear Model tests comparing great tit first egg date, chick mean mass and chick biomass at the CUBG to Wicken Fen, Cow Lane, Brampton Wood and small woods. Note: a negative parameter estimate for egg date represents an earlier first egg date than at the CUBG and a positive parameter estimate represents a later first egg date than at the CUBG. For mean mass and biomass a negative parameter estimate represents a lighter mass than at the CUBG and a positive parameter estimate represents a heavier mass than at the CUBG.

Response variable	Site (N) by site (N)		Parameter estimate	*t* value	Standard error
Egg date	Botanic Gardens (59)	Wicken Fen (44)	2.03	0.936	2.16
		Cow Lane (133)	4.41	2.21*	1.99
		Brampton Wood (104)	1.75	0.81	2.16
		Small woods (133)	4.64	2.26*	2.05
Mean mass	Botanic Gardens (48)	Wicken Fen (18)	2.74	2.97**	0.92
		Cow Lane (109)	0.83	0.99	0.85
		Brampton Wood (91)	3.00	3.35***	0.90
		Small woods (117)	1.36	1.57	0.87
Biomass	Botanic Gardens (46)	Wicken Fen (18)	38.91	5.86***	6.64
		Cow Lane (108)	25.44	6.22***	4.09
		Brampton Wood (84)	47.79	10.75***	4.45
		Small woods (103)	20.84	4.50***	4.64

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, ^{1} $P \leq 0.10$,

Table 4.6 Parameter estimates generated by Generalised Linear Model tests with Poisson regression and log link comparing blue tit clutch size and number of chicks fledged at CUBG to Wicken Fen, Cow Lane, Brampton Wood, Wennington Wood and small woods. Note: a negative parameter estimate represents a smaller clutch size or lower number of chicks fledging than at the CUBG and a positive parameter estimate represents a larger clutch size or higher number of chicks fledging than at the CUBG.

Response variable	Site (N) by site (N)		Parameter estimate	Wald χ^2	Standard error
Clutch size	Botanic Gardens (66)	Wicken Fen (20)	0.02	0.23	0.04
		Cow Lane (86)	0.02	0.71	0.03
		Brampton Wood (19)	0.17	21.82***	0.04
		Wennington Wood (59)	0.18	46.34***	0.03
		Small woods (74)	0.18	55.48***	0.02
Number fledged	Botanic Gardens (63)	Wicken Fen (13)	1.45	26.20***	0.28
		Cow Lane (68)	-0.15	0.47	0.22
		Brampton Wood (18)	0.42	3.60[1]	0.22
		Wennington Wood (56)	0.36	3.26[1]	0.20
		Small woods (66)	0.20	1.05	0.19

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, [1] $P \leq 0.10$,

Table 4.7 Parameter estimates generated by Generalised Linear Model tests with Poisson regression and log link comparing great tit clutch size and number of chicks fledged at the CUBG to Wicken Fen, Cow Lane, Brampton Wood and small woods. Note: a negative parameter estimate represents a smaller clutch size or lower number of chicks fledging than at the CUBG and a positive parameter estimate represents a larger clutch size or higher number of chicks fledging than at the CUBG.

Response variable	Site (N) by site (N)		Parameter estimate	Wald χ^2	Standard error
Clutch size	Botanic Gardens (52)	Wicken Fen (18)	0.35	10.53***	0.11
		Cow Lane (112)	0.22	7.42**	0.08
		Brampton Wood (88)	0.45	27.76***	0.08
		Small woods (101)	0.49	34.30***	0.08
Number fledged	Botanic Gardens (52)	Wicken Fen (18)	0.35	2.66	0.22
		Cow Lane (112)	-0.03	0.03	0.17
		Brampton Wood (88)	0.36	4.48*	0.17
		Small woods (101)	0.23	1.77	0.17

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, ^{1} $P \leq 0.10$,

Table 4.8 Parameter estimates generated by Generalised Linear Model tests with binomial regression and logit link comparing blue tit fledging success at the CUBG to Wicken Fen, Cow Lane, Brampton Wood, Wennington Wood and small woods. Note: a negative parameter estimate represents a lower proportion of chicks fledging than at the CUBG and a positive parameter estimate represents a higher proportion of chicks fledging than at the CUBG.

Response variable	Trials variable	Site (N) by site (N)		Parameter estimate	Wald χ^2	Standard error
Number fledged	Clutch size	Botanic Gardens (63)	Wicken Fen (13)	3.35	32.47***	0.59
			Cow Lane (68)	-0.38	1.16	0.36
			Brampton Wood (18)	2.62	6.32**	1.04
			Wennington Wood (56)	1.35	7.59**	0.49
			Small woods (66)	0.55	2.27	0.37

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, ^{1} $P \leq 0.10$,

Table 4.9 Parameter estimates generated by Generalised Linear Model tests with binomial regression and logit link comparing great tit fledging success at the CUBG to Wicken Fen, Cow Lane, Brampton wood and small woods. Note: a negative parameter estimate represents a lower proportion of chicks fledging than at the CUBG and a positive parameter estimate represents a higher proportion of chicks fledging than at the CUBG.

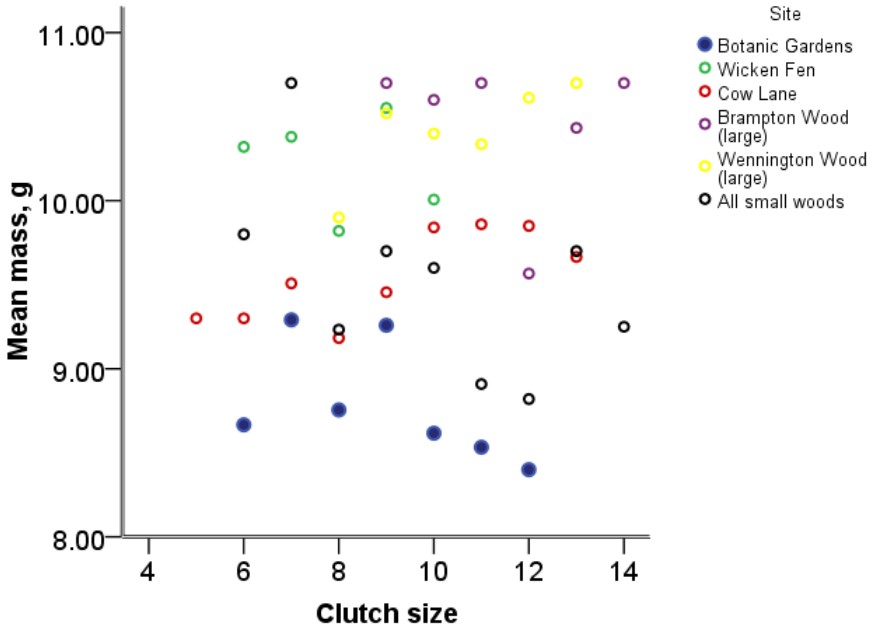
Response variable	Trials variable	Site (N) by site (N)		Parameter estimate	Wald χ^2	Standard error
Number fledged	Clutch size	Botanic Gardens (52)	Wicken Fen (18)	3.34	17.90***	0.79
			Cow Lane (112)	-0.20	0.28	0.38
			Brampton Wood (88)	1.90	12.53***	0.54
			Small woods (101)	0.72	3.10[1]	0.41

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, [1] $P \leq 0.10$,

Figure 4.2 Relationship between clutch size and mean chick mass of blue tits and great tits breeding in different habitats. Mean values are shown for each clutch size for each habitat type. Data shown are pooled across years (2000-2009 for blue tits and 2003-2009 for great tits for Cow Lane, 2003-2009 for the CUBG, Brampton Wood, Wennington Wood (blue tit only) and all small woods and 2007-2008 for Wicken Fen for both species). Note: mean mass in the figure refers to the average of the mean mass.

Blue tit

a) Mean mass and clutch size



Great tit

b) Mean mass and clutch size

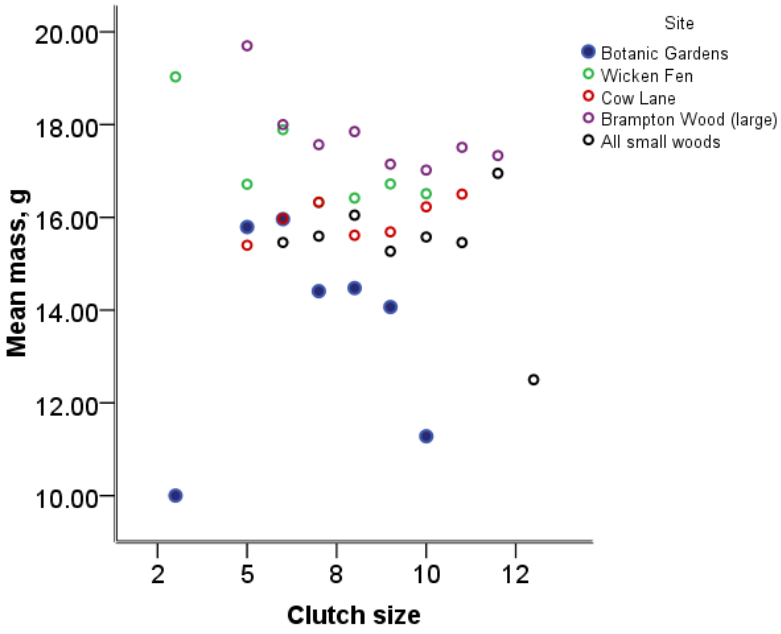
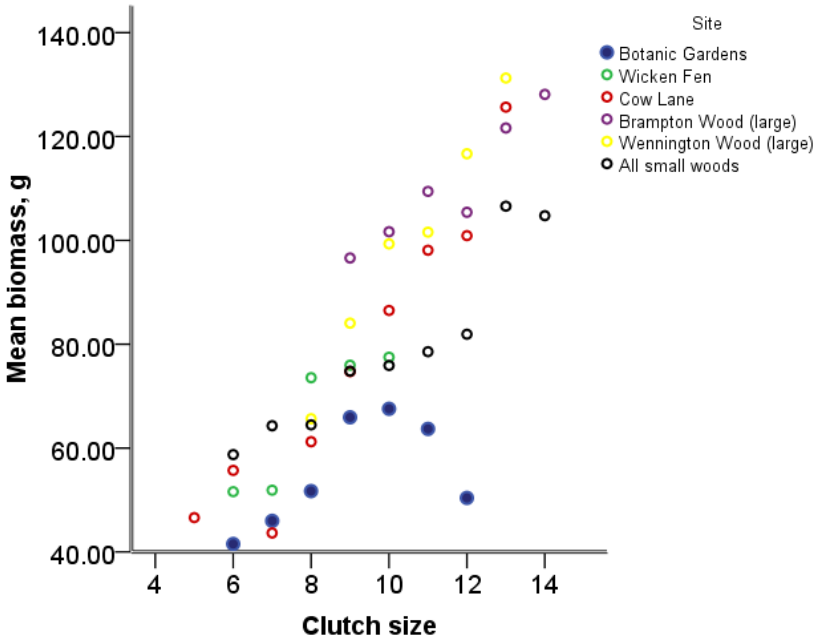


Figure 4.3 Relationship between clutch size and chick biomass of blue tits and great tits breeding in different habitats. Mean values are shown for each clutch size for each habitat type. Data shown are pooled across years (2000-2009 for blue tits and 2003-2009 for great tits for Cow Lane, 2003-2009 for the CUBG, Brampton Wood, Wennington Wood (blue tit only) and all small woods and 2007-2008 for Wicken Fen for both species).

Blue tit

a) Biomass and clutch size



Great tit

b) Biomass and clutch size

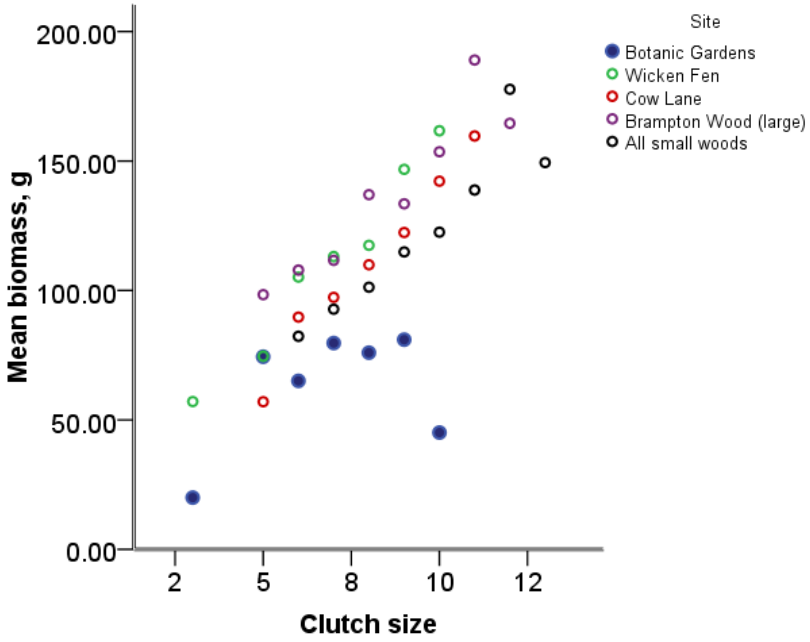
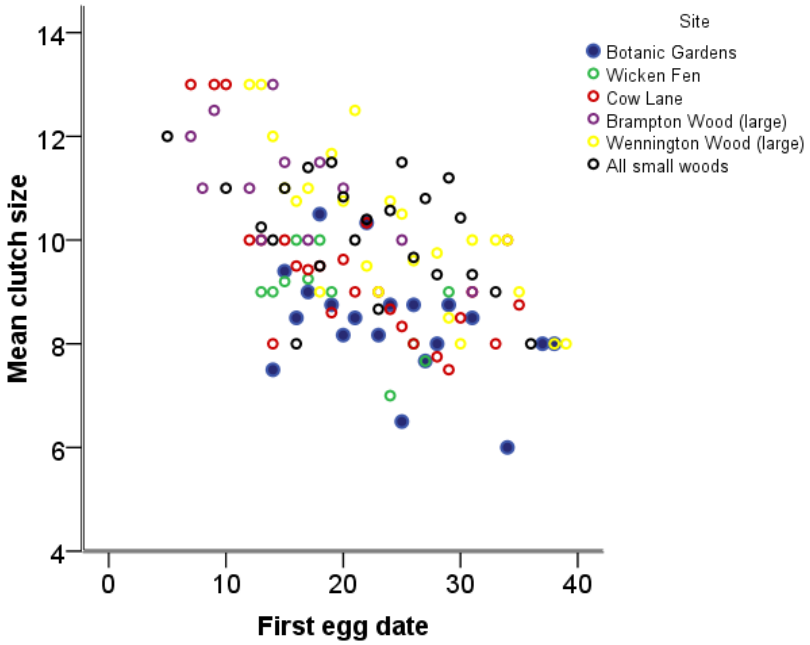


Figure 4.4 Relationship between first egg dates and clutch size of blue tits and great tits breeding in different habitats. Mean values are shown for each first egg date for each habitat type. Data shown are pooled across years (2000-2009 for blue tits and 2003-2009 for great tits for Cow Lane, 2003-2009 for the CUBG, Brampton Wood, Wennington Wood (blue tit only) and all small woods and 2007-2008 for Wicken Fen for both species).

Blue tit

a) Clutch size and first egg date



Great tit

b) Clutch size and first egg date

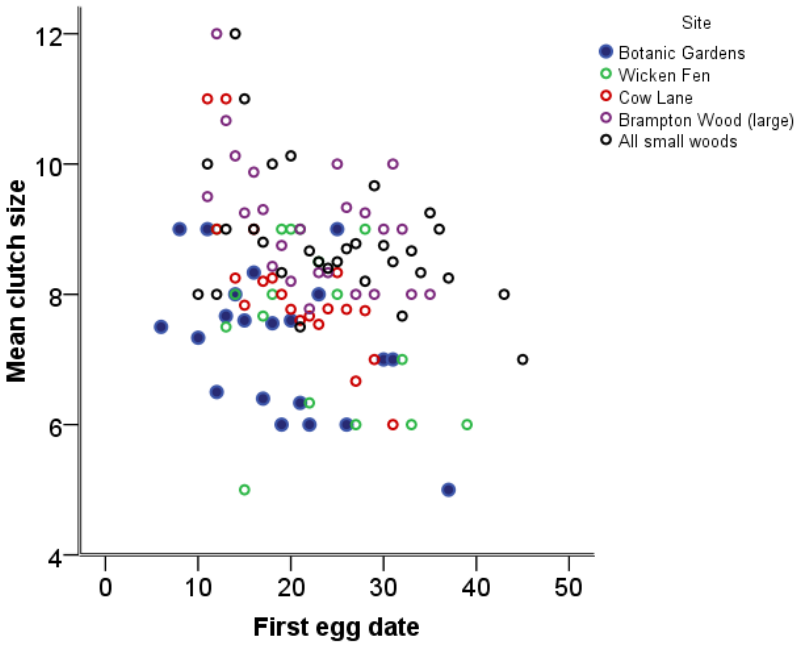
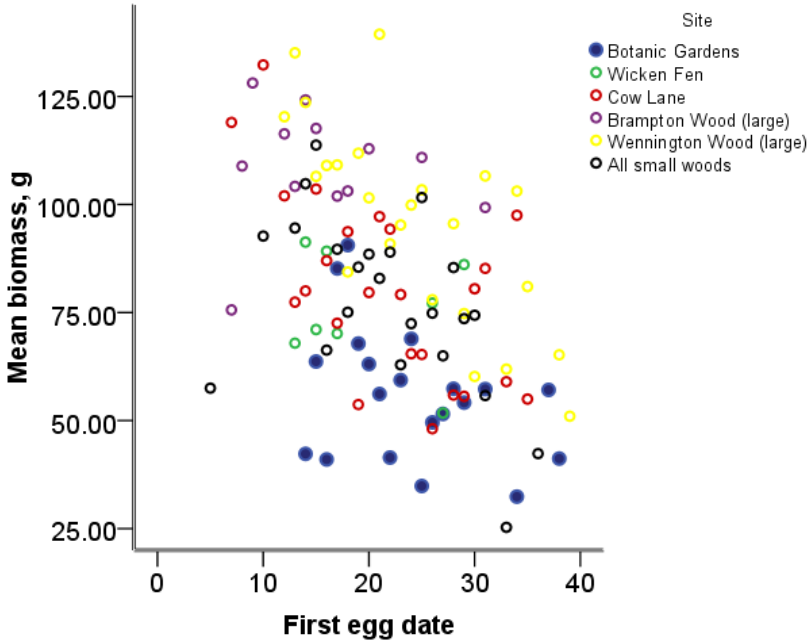


Figure 4.5 Relationship between first egg dates and chick biomass of blue tits and great tits breeding in different habitats. Mean values are shown for each first egg date for each habitat type. Data shown are pooled across years (2000-2009 for blue tits and 2003-2009 for great tits for Cow Lane, 2003-2009 for the CUBG, Brampton Wood, Wennington Wood (blue tit only) and all small woods and 2007-2008 for Wicken Fen for both species).

Blue tit

a) Biomass and first egg date



Great tit

b) Biomass and first egg date

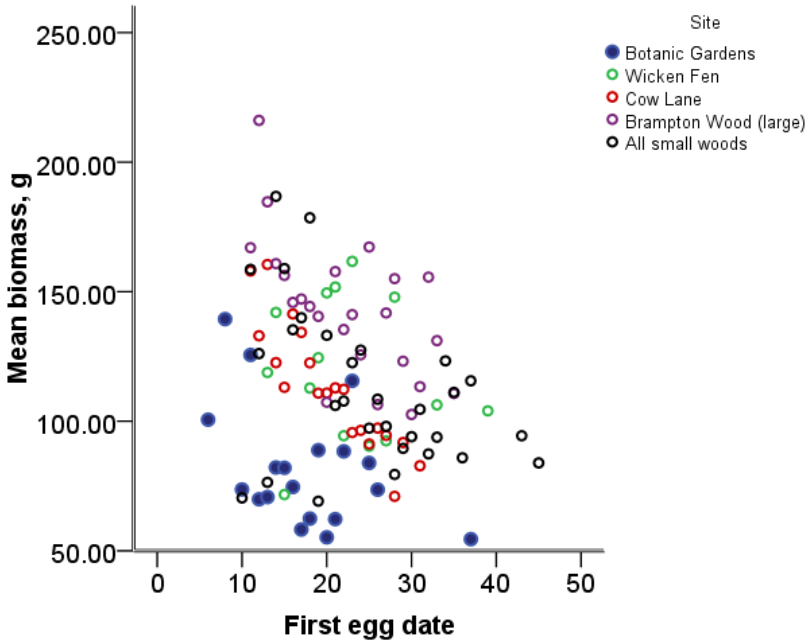


Figure 4.6 Relationship between first egg dates and mean number of blue tit chicks fledging in different habitats. Mean values are shown for each first egg date for each habitat type. Data shown are pooled across years (2000-2009 for Cow Lane, 2003-2009 for the CUBG, Brampton Wood, Wennington Wood and all small woods and 2007-2008 for Wicken Fen). Note the relationship for number fledged/egg date for great tits was not significant and hence is not shown.

Blue tit

Number fledged and first egg date

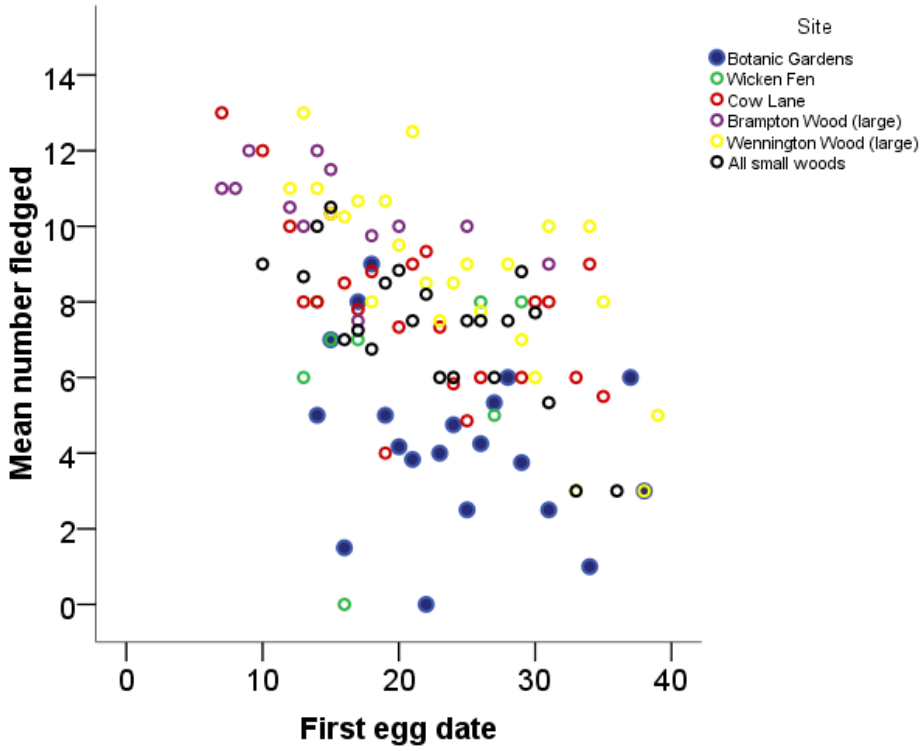
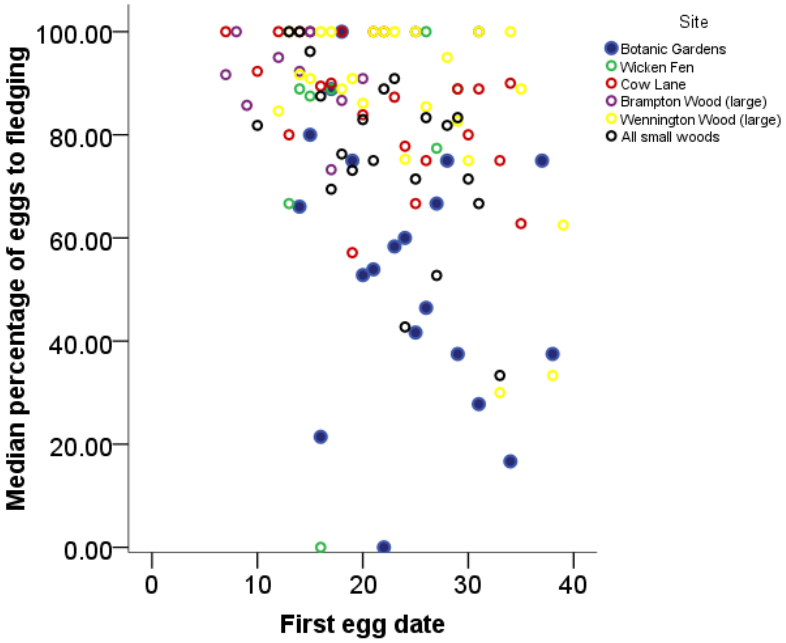


Figure 4.7 Relationship between first egg dates and percentage of blue tit and great tit chicks fledging in different habitats. Median values are shown for each first egg date for each habitat type. Data shown are pooled across years (2000-2009 for blue tits and 2003-2009 for great tits for Cow Lane, 2003-2009 for the CUBG, Brampton Wood, Wennington Wood (blue tit only) and all small woods and 2007-2008 for Wicken Fen for both species).

Blue tit

a) Percentage fledged and first egg date



Great tit

b) Percentage fledged and first egg date

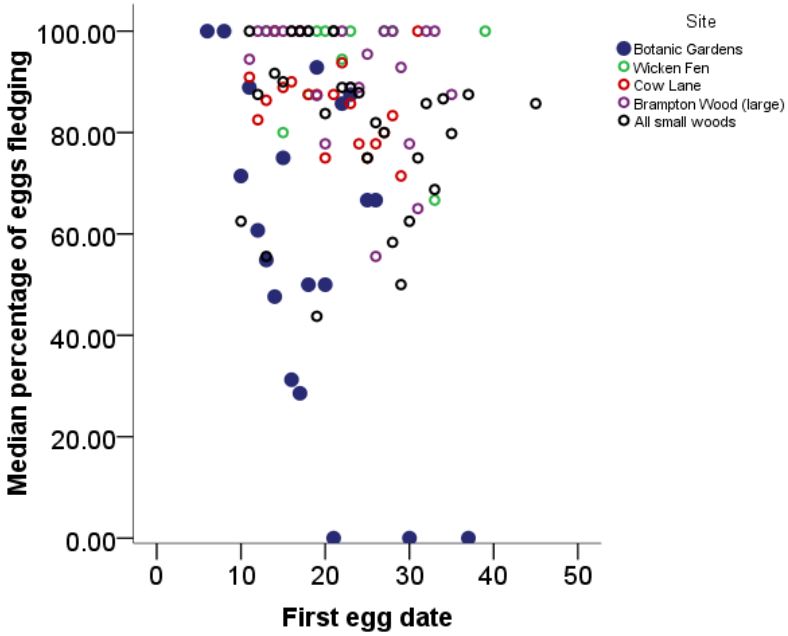
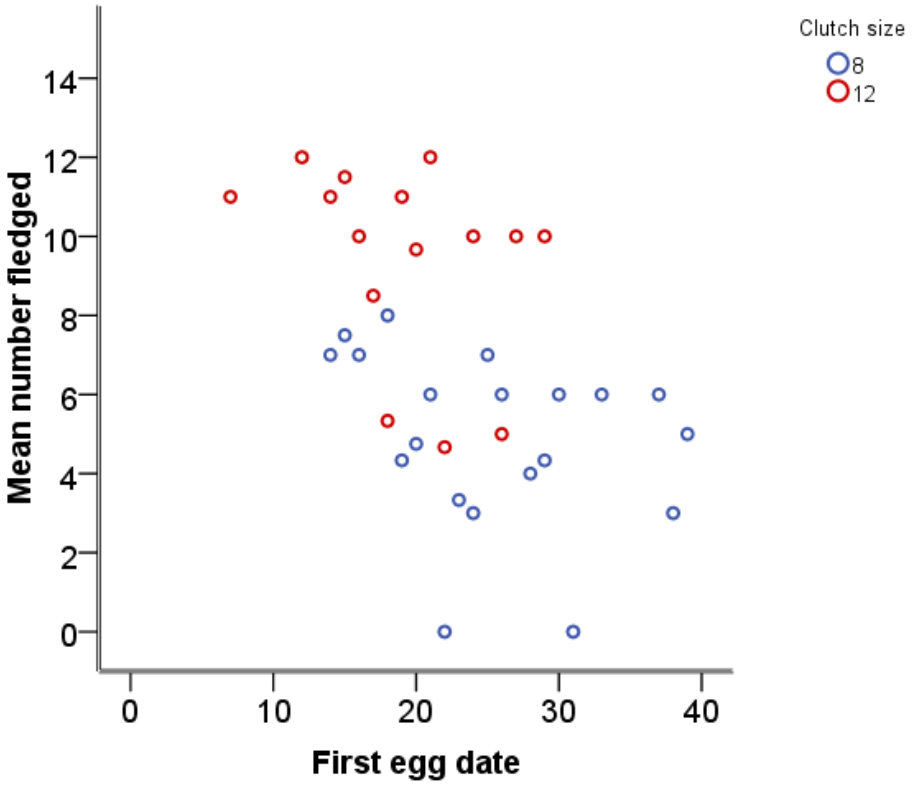


Figure 4.8 Example of interactions between first egg date and clutch size. The figure shows the mean number of blue tit chicks that fledged with different first egg dates and clutch sizes of 8 and 12. Data are pooled across sites and across years (2000-2009 for Cow Lane, 2003-2009 for the CUBG, Brampton Wood, Wennington Wood and all small woods and 2007-2008 for Wicken Fen). Only two clutch sizes are shown for clarity.



4.3.2 Habitat and reproductive success within the CUBG

Table 4.10 summarises the results from the Generalised Linear Model (with binomial distribution) testing the fledging success between blue tits and great tits within the CUBG and shows that the two species do not differ in their fledgling success. The difference in fledging success (proportion of eggs to fledging) between years and the species x year interaction suggests that in some years one species may have had greater fledging success than the other and or visa versa in other years.

The relationship between reproductive success and the habitat around a nest box is summarised in Table 4.11 for blue tits and in Table 4.12 for great tits. For both species there was no significant relationship between clutch size and any of the habitat types around a nest box for either of the buffer sizes (25m or 100m radius).

For blue tits, the mean mass of chicks was significantly related to the percentage of 1) non-native trees and shrubs (mostly negative, Figure 4.9a), 2) native trees and shrubs (mostly positive or neutral, Figure 4.9b), and 3) gaps (mixed, Figure 4.9c) within a 25m radius of a nest box. The percentage of 1) evergreen trees and shrubs (mixed, Figure 4.10a), 2) deciduous trees and shrubs (mixed, Figure 4.10b), and 3) gaps (mostly negative, Figure 4.10c) within the same radius were significantly related to blue tit chick biomass. This result was not evident with the 100m radius around a nest box suggesting that these habitat types have a greater influence on reproductive success when closer to the nest box.

Mean chick mass was significantly related to the percentages of *Quercus* (mixed, Figure. 4.11a) and of *Betula* (mostly positive or neutral, Figure 4.11b) within a 100m radius of a nest box, and chick biomass to percentage of *Quercus* (mixed, Figure 4.12)

only. However, this effect was not seen within a 25m radius of the nest box which may have been a consequence of very low percentages of *Quercus* and *Betula* being available for many of the boxes within this area.

Figures 4.9 to 4.12 illustrate the relationships between habitat type and mean chick mass and chick biomass for all significant models and show that it is highly variable and inconsistent across years. This explains why interactions between habitat type and year were significant for all models in Figures 4.9 and 4.10 and for the model shown in Figure 4.12.

For great tits the only habitat type to have a significant effect on reproductive performance (mean chick mass) was the percentage of native trees and shrubs within a 25m radius of the box (Table 4.12). Figure 4.13 illustrates the relationships between mean chick mass and habitat type in this model and shows that mean chick mass generally increased as the percentage of native trees and shrubs increased. Year was a significant factor in this model and this variation is also shown in Figure 4.13; there was little relationship between habitat type and mean chick mass in 2008.

Some habitat types approached significance; the percentage of *Quercus* within a 25m radius of the box having a near significant effect on mean chick mass ($P < 0.10$) and the percentage of non-native trees and shrubs within a 100m radius of the box having a near significant effect on chick biomass ($P < 0.10$) (Table 4.12).

Table 4.10 Comparison of fledging success between blue and great tits within the CUBG using Generalised Linear Models with binomial regression and logit link.

Response variable	Trials variable	Wald chi-square test of model effects			Omnibus test		Final model equation
		Species	Year	Species x Year interactions	Likelihood ratio chi-square		
No. fledged	Clutch size	0.49	51.66***	30.32***	105.75***	13 *df*	Species + Year + Specie X Year

Table 4.11 Summary of Mixed Models describing the relationships between different habitat variables and blue tit breeding success (clutch size, mean mass and biomass of chicks) within the CUBG.

Habitat type		Response variable	F value for type III tests of fixed effects						Estimates of covariance parameters	
			Habitat		Year		Habitat x Year interaction		Nest box	
			25m	100m	25m	100m	25m	100m	25m	100m
Non-native trees and shrubs		Clutch size	0.15	0.01	0.63	0.89	1.19	1.27	1.49	1.55
		Mean mass	12.50***	0.23	2.82*	1.23	3.23*	1.18	0.61	✦
		Biomass	3.12[1]	0.01	3.78**	2.67*	2.78*	2.36[1]	45.98	111.38
Native trees and shrubs		Clutch size	0.40	0.05	3.46*	2.70*	1.64	1.70	1.45	2.09
		Mean mass	10.50**	0.27	4.72**	2.41[1]	2.82*	2.14[1]	0.48	0.40
		Biomass	2.84[1]	1.37	3.11*	1.97	2.86*	2.68*	38.11	15.84
Gap		Clutch size	0.04	1.42	0.82	1.11	2.28[1]	1.05	1.68	1.56
		Mean mass	6.11*	3.54[1]	2.93*	2.34[1]	4.01**	3.19*	0.11	0.11
		Biomass	4.54*	0.25	2.33[1]	2.38[1]	2.77*	2.61*	66.11	✦
Genera type	*Quercus*	Clutch size	0.13	0.01	1.47	2.83*	0.63	1.15	1.58	1.57
		Mean mass	0.02	5.73*	2.05[1]	2.10[1]	0.61	1.44	0.09	0.48
		Biomass	3.80[1]	6.06*	3.20*	5.23***	†	4.38**	22.28	48.28
	Betula	Clutch size	0.08	0.08	3.24*	3.24*	1.17	1.17	1.94	1.94
		Mean mass	1.00	4.21*	3.54**	1.78	1.58	0.89	0.29	0.36
		Biomass	1.16	2.10	4.27**	2.66*	3.12*	1.62	37.52	52.12
	Acer	Clutch size	0.37	0.73	2.06[1]	2.30[1]	0.82	1.96	1.68	1.70
		Mean mass	0.67	0.15	6.12***	2.73*	4.50**	2.10	0.53	0.56
		Biomass	0.7	1.06	0.94	0.76	0.78	1.40	39.38	50.12
Evergreen trees and shrubs		Clutch size	0.23	0.77	0.89	1.41	1.49	1.36	2.22	1.99
		Mean mass	2.21	0.47	2.79*	1.83	2.65*	1.85	0.29	0.36
		Biomass	6.42*	0.78	6.17***	2.62*	4.30**	2.03[1]	27.89	✦
Deciduous trees and shrubs		Clutch size	0.29	1.58	2.53	1.94	1.70	1.94	2.21	2.09
		Mean mass	1.77	1.77	2.48*	3.74*	2.12[1]	3.61*	0.27	0.34
		Biomass	5.34*	3.71[1]	2.67*	1.75	3.13*	2.38[1]	26.28	✦

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, [1] $P \leq 0.10$, † not significant and removal of which led to significance in other variable(s), ✦ estimate is redundant.

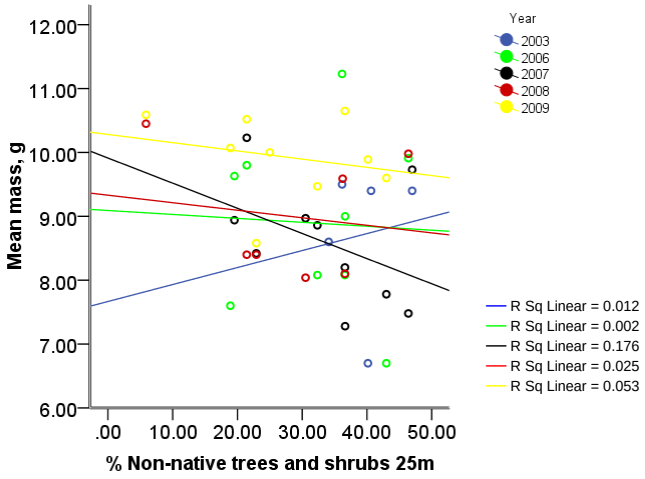
Table 4.12 Summary of Mixed Models describing the relationships between different habitat variables and great tit breeding success (clutch size, mean mass and biomass of chicks) within the CUBG.

Habitat type		Response variable	F value for type III tests of fixed effects						Estimates of covariance parameters	
			Habitat		Year		Habitat x Year interaction		Nest box	
			25m	100m	25m	100m	25m	100m	25m	100m
Non-native trees and shrubs		Clutch size	0.06	0.86	0.60	0.32	0.56	0.25	2.43	0.85
		Mean mass	0.22	0.47	0.19	0.49	0.33	0.36	1.72	1.22
		Biomass	0.70	3.24¹	0.49	1.92	0.43	1.89	✦	✦
Native trees and shrubs		Clutch size	0.00	0.00	0.43	0.21	0.34	0.58	1.27	1.27
		Mean mass	5.30*	0.04	5.03**	1.62	†	0.72	0.58	2.2
		Biomass	0.79	2.67	1.52	2.13	1.61	2.27	✦	✦
Gap		Clutch size	0.08	0.11	1.24	1.73	0.29	0.86	2.01	1.67
		Mean mass	0.11	1	1.37	2.74	1.23	3.39¹	1.90	4.30
		Biomass	0.09	1.95	2.77¹	0.56	2.81¹	0.77	✦	✦
Genera type	*Quercus*	Clutch size	0.28	0.13	2.30	0.47	0.48	0.49	1.97	1.52
		Mean mass	3.63¹	0.55	6.42**	1.04	3.12¹	0.17	3.16	1.47
		Biomass	0.01	0.22	0.66	0.44	0.16	0.72	✦	✦
	Betula	Clutch size	0.00	0.08	1.06	0.86	0.78	0.7	1.94	1.59
		Mean mass	2.09	1.21	2.95¹	2.25	0.61	0.65	0.77	1.1
		Biomass	0.27	1.28	2.61¹	3.08*	3.26*	3.17*	✦	✦
	Acer	Clutch size	0.02	0.04	1.61	0.66	0.18	0.75	1.63	1.35
		Mean mass	0.19	0.23	3.91*	2.52	0.92	0.9	1.45	2.2
		Biomass	0.04	1.81	0.90	0.54	0.72	0.49	✦	✦
Evergreen trees and shrubs		Clutch size	2.84	0.97	0.92	0.59	0.27	0.31	0.82	0.68
		Mean mass	0.65	0.29	1.40	0.50	0.44	0.27	1.36	1.59
		Biomass	2.89	1.25	1.01	1.48	1.37	1.52	✦	✦
Deciduous trees and shrubs		Clutch size	1.20	0.23	0.55	0.49	0.36	0.73	1.09	1.72
		Mean mass	2.62	0	2.68	1.39	0.88	0.86	1.13	2.04
		Biomass	1.41	1.98	1.83	2.17	2.02	2.22	✦	✦

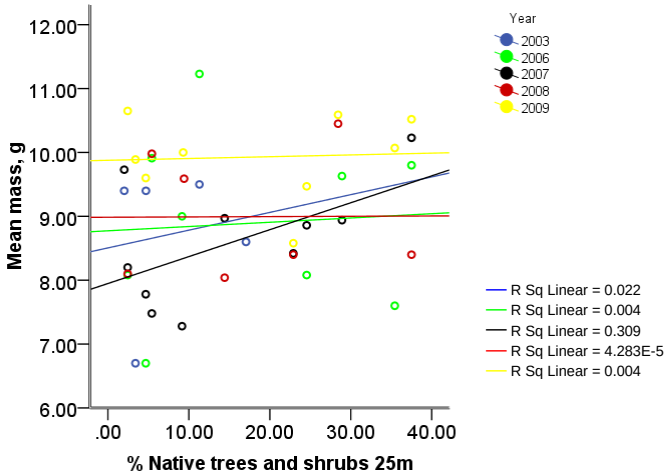
*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, ¹ $P \leq 0.10$, † not significant and removal of which led to significance in other variable(s), ✦ estimate is redundant.

Figure 4.9 Relationships between habitat type within a 25 m radius around a nest box and blue tit mean chick mass in the CUBG for each year (2003 and 2006-2009); note: mean mass in the figure refers to the average of the mean mass. Data for 2004 and 2005 were removed from the Figure due to small samples sizes.

a) Mean mass and % non-native trees and shrubs



b) Mean mass and % native trees and shrubs



c) Mean mass and % gaps

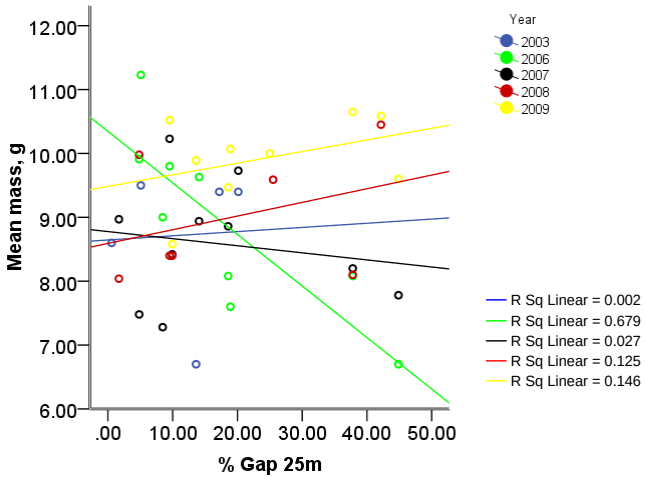
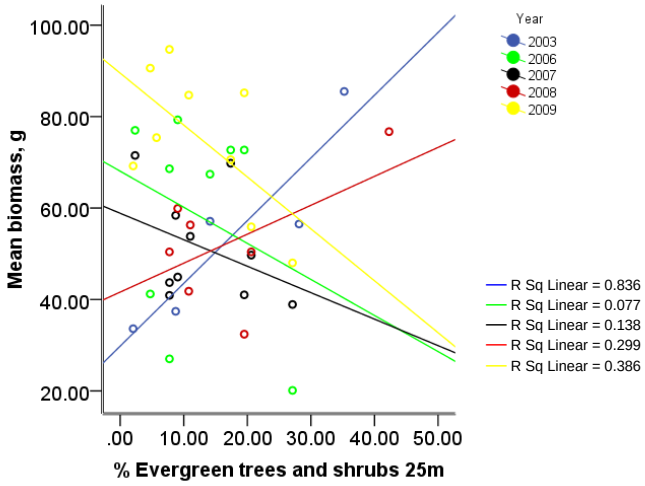
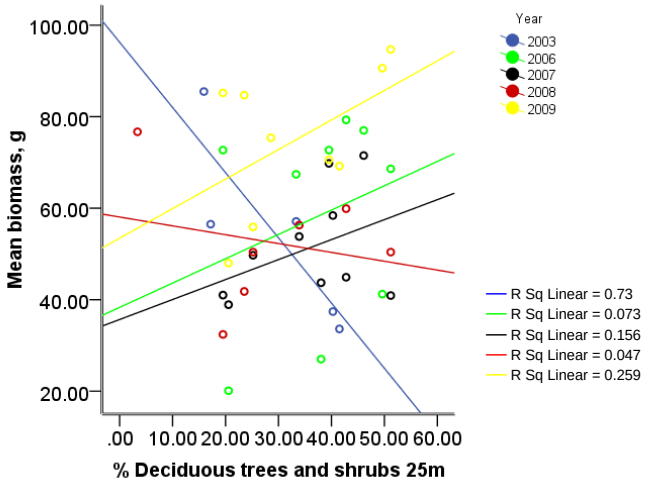


Figure 4.10 Relationships between habitat type within a 25 m radius around a nest box and blue tit mean chick biomass in the CUBG for each year (2003 and 2006-2009). Data for 2004 and 2005 were removed from the Figure due to small samples sizes

a) Mean biomass and % evergreen trees and shrubs



b) Mean biomass and % deciduous trees and shrubs



c) Mean biomass and % gaps

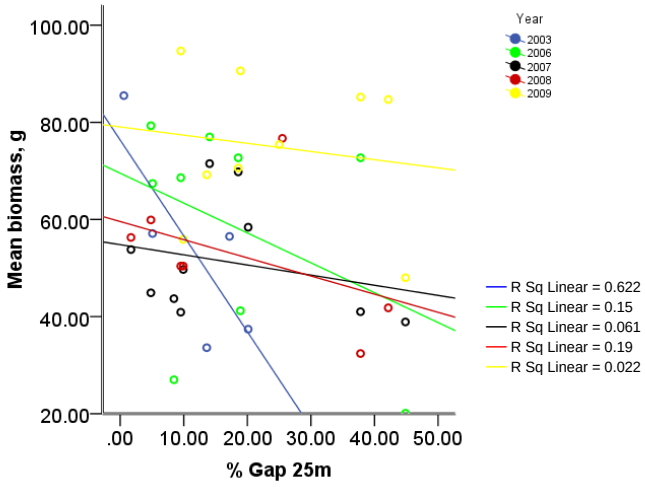
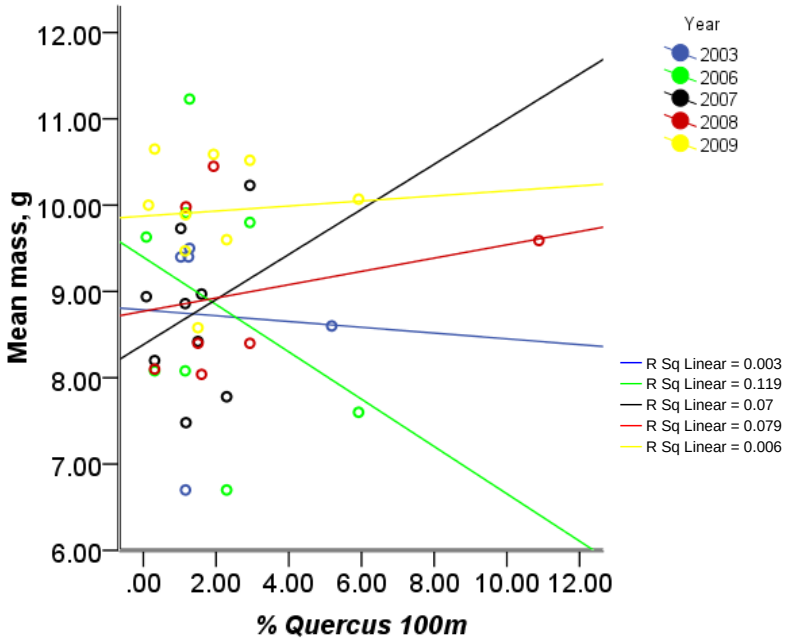


Figure 4.11 Relationships between habitat type within a 100 m radius around a nest box and blue tit mean chick mass in the CUBG for each year (2003 and 2006-2009). Note: mean mass in the figure refers to the average of the mean mass. Data for 2004 and 2005 were removed from the Figure due to small samples sizes

a) Mean mass and % *Quercus*



b) Mean mass and % *Betula*

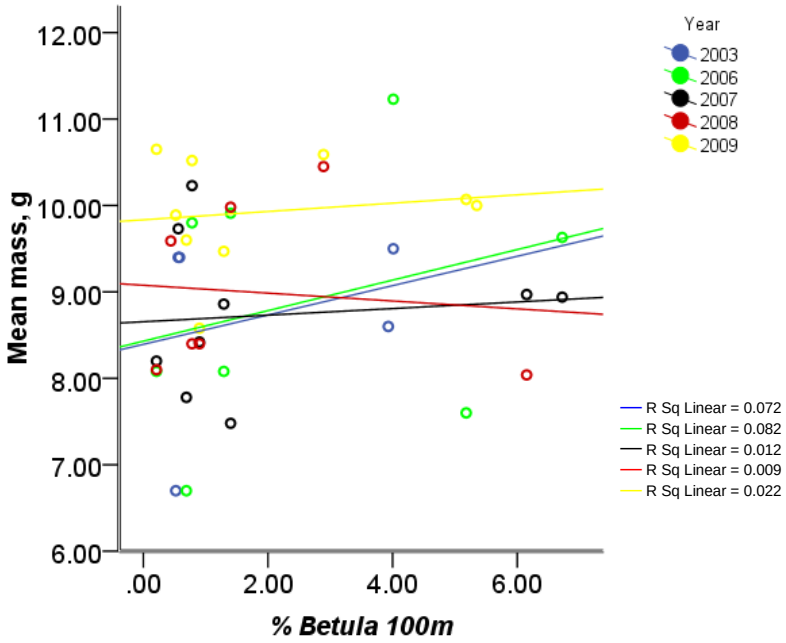


Figure 4.12 Relationships between habitat type within a 100 m radius around a nest box and blue tit mean chick biomass in the CUBG for each year (2003 and 2006-2009). Data for 2004 and 2005 were removed from the Figure due to small samples sizes

Mean biomass and % *Quercus*

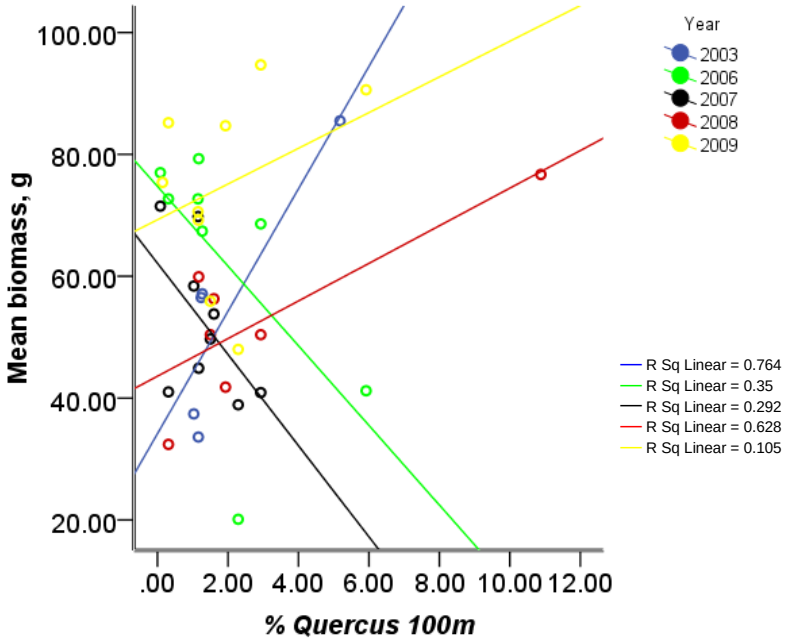
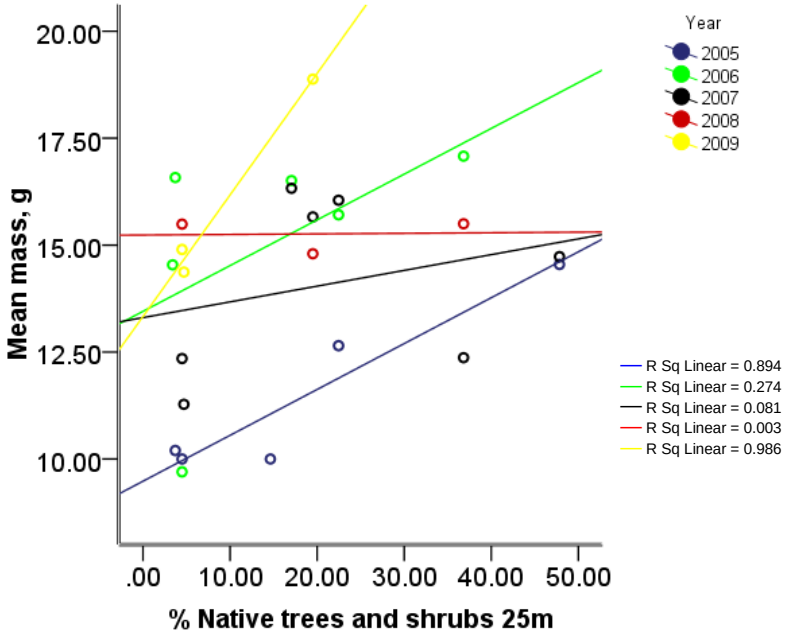


Figure 4.13 Relationships between habitat type within a 25 m radius around a nest box and great tit mean chick mass in the CUBG for each year (2005-2009); note: mean mass in the figure refers to the average of the mean mass. Data for 2003 and 2004 were removed due to small samples sizes.

Mean mass and % native trees and shrubs



4.4 Discussion

Mixed, General and Generalised Linear Models are a useful modern tool to test for differences in reproductive success of birds across sites where, for example, variation in first egg dates both between and within sites may have confounded results. Now tests can be made that account for multiple correlated factors explaining variables such as chick mass and biomass. From these tests, blue tits and great tits were shown to differ between sites in all reproductive parameters (clutch size, mean chick mass, chick biomass, number of chicks fledging and fledging success) and overall had the greatest reproductive success in large woods. Within the CUBG, mean mass and biomass of chicks in blue tits was affected more by the microhabitat surrounding a nest box compared to the mean mass and biomass of great tit chicks.

4.4.1 Reproductive success in different habitats

In relation to the CUBG, reproductive parameters varied in their significance from other sites but in general reproductive performance was poor with great tits performing worse than blue tits. Table 4.13 below summarises these differences and can be referred to throughout section 4.4.1 of this discussion:

Table 4.13 A summary of the main differences between the CUBG and the other sites (Cow Lane, Wicken Fen, small woods, Brampton Wood and Wennington Wood (blue tit only) in relation to blue tit and great tit reproductive parameters. Bold text with a * indicates a significant difference.

		Reproductive succes compared to the CUBG site					
Species	Site	Egg date	Clutch size	Mean chick mass	Chick biomass	Number of chicks fledging	Fledging success (% chicks fledging)
Blue tit	Cow Lane	Later	Larger	Lighter	**Higher***	Lower	Lower
	Wicken Fen	Earlier	Larger	**Heavier***	**Higher***	**Higher***	**Higher***
	Small woods	Earlier	**Larger***	Lighter	**Higher***	Higher	Higher
	Brampton Wood	**Earlier***	**Larger***	Heavier	**Higher***	Higher	**Higher***
	Wennington Wood	**Earlier***	**Larger***	Heavier	**Higher***	Higher	**Higher***
Great tit	Cow Lane	**Later***	**Larger***	Heavier	**Higher***	Lower	Lower
	Wicken Fen	Later	**Larger***	**Heavier***	**Higher***	Higher	**Higher***
	Small woods	**Later***	**Larger***	Heavier	**Higher***	Higher	Higher
	Brampton Wood	Later	**Larger***	**Heavier***	**Higher***	**Higher***	**Higher***

Both species had reduced clutch sizes at the CUBG with great tits having significantly smaller clutches than at all other sites and blue tits having significantly smaller clutches than at woodland sites (large and small). This is not surprising; in marginal habitats clutch sizes are often smaller (Cowie and Hinsley 1987; Hinsley *et al.* 2008, 2009; Perrins 1979) and smaller clutch sizes have been attributed to low caterpillar abundance (Belda *et al.* 1998; Blondel *et al*. 1993; Perrins and McCleery 1989). In fact brood manipulation studies have shown that offspring in artificially enlarged broods were of lower quality (Blondel *et al*. 1998). Also, broods enlarged by three chicks in poor quality habitat suffered significantly reduced chick growth compared with rich habitats, where there was no effect, and this was attributed to differences in food abundance (Tremblay *et al.* 2003). A similar effect can be seen in the CUBG for both blue tits and great tits in Figure 4.1 where, when the clutches were large (10 for great tits and 12 for blue tits), biomass dropped sharply. This indicates an inability to raise a large brood in the CUBG, with a large number of chicks perishing, and points to a food poor habitat. In addition, large clutches (10 eggs) were associated with reduced mean masses (as low

as 11g in great tits). The effect was less pronounced for blue tits, indicating that the habitat in the CUBG has a greater negative effect on great tits.

In addition, brood biomass was significantly lower for both species in the CUBG than all other sites. Fledging success was also significantly lower for both species compared with large woods and Wicken Fen, and for great tits lower than in small woods. This may indicate that clutch sizes, although reduced, are still too large to be optimal in the CUBG with both species of tits struggling to feed their chicks. Mass at fledging is a good indicator of later survival with heavier chicks more likely to survive (e.g. Cichon and Lindén 1995; Naef-Daenzer *et al*. 2001; Perrins 1965), therefore, although the lighter blue tit chicks in a nest may make it to fledging at the CUBG, their chances of survival to recruitment may be less than for chicks fledging in the marginal habitat at Cow Lane. Great tits similarly, although having reduced clutch sizes at the CUBG, still reared chicks with lower mean masses than at Wicken Fen and Brampton wood. This suggests that clutch size in the CUBG in both species is maladaptive.

Maladaptive clutch sizes have been discussed by other authors (e.g. Blondel *et al*. 1998; Loman 2003). It may be that despite laying smaller clutches in the CUBG, blue tits and great tits are unable to reduce them further due to gene flow from other populations, preventing genetic adaptation. However, Partecke *et al.* 2004 found that in blackbirds reproductive parameters such as laying date were mainly affected by phenotypic rather than genetic differences. In addition, Björklund *et al*. 2010 showed that parks had higher genetic variation than forests, suggesting the populations were not genetically isolated. The tits in the CUBG therefore may only be able to adapt phenotypically to environmental conditions to a certain degree but are not able to adapt genotypically due to continual influx of individuals from populations from elsewhere.

Although great tits at the CUBG and Wicken Fen fledged similar numbers of chicks, the proportional success (as well as clutch size) was greater at Wicken Fen. It was possible that the relatively small sample size (N=18) used for the fledging tests (number and success) at Wicken Fen was associated with a lower mean clutch size than the overall clutch size at Wicken Fen and hence had the effect of reducing numbers fledged (mean clutch for the sample of 18 was 7.2 whereas the overall mean for Wicken was 7.68, and the overall mean for CUBG was 7.2). This may have occurred due to the high predation rate at Wicken which reduced the sample size of nests with fledglings compared to that with full clutches. Of the surviving 18 nests, 17 had 100% fledging success, creating the difference with the CUBG. However, this difference may also reflect genuine habitat differences between the sites.

Blue tits and great tits at the CUBG had poorer reproductive success when compared to the marginal habitat of Wicken Fen, having both lighter chicks and lower fledging success. Structurally these two sites are similar, having shrub layers interspersed with trees, and thus the main difference between the two appears to be in plant composition, with the CUBG being dominated by a large proportion of exotics. This could point towards the idea that 'functional gaps' (inappropriate foraging substrates) as well as 'structural gaps' (physical gaps) (see Hinsley *et al*. 2009) exacerbate the poor reproductive success in the CUBG.

In fact, reproductive performance was good at Wicken Fen. In blue tits, Wicken Fen was the only site that had significantly heavier chicks than at the CUBG, despite no difference in clutch size. There was no difference in chick mass between the CUBG and other sites, even the large woodlands, which was surprising, but probably a consequence of smaller clutch size (and hence also smaller biomass) in the CUBG. It is possible at Wicken Fen that the predominance of willow creates a more even supply of caterpillar

prey across the whole season rather than a discrete peak as in oak woodland. Willow has been shown to be rich in caterpillars, being ranked 3rd behind oaks and cherry trees (Tallamy and Shropshire 2009). Additionally, Niemelä *et al.* (1982) argue that, on the trees they tested, they only found oaks and bird cherries to have a spring peak of caterpillars due to these trees in spring ceasing production of young leaves, which are preferred by some lepidopterous larvae. However, on (as they describe) '*Populus* type' trees (*Populus*, *Betula*, *Alnus*), young leaves are produced throughout the growing season and so attract lepidopteran larvae that can feed on both mature and young leaves. Therefore the availability of lepidopteran larvae on willows may be more evenly distributed across the whole of the breeding season. This may result in chick mass being less variable across the season as food availability is not so constrained to one peak. In contrast, chicks in the nest in oak woodland which "miss" the main caterpillar peak may have a lower mass due to the poorer foraging conditions and this could then affect the overall mean for the site.

However, it is surprising that Cow Lane is not as different in reproductive performance compared to the CUBG as is Wicken Fen, with mean chick mass and fledging success (as well as some other reproductive parameters) in both species not differing significantly to the CUBG. Cow Lane and Wicken Fen appear to be very similar habitats, but Wicken Fen appears to be better habitat for breeding birds than Cow Lane. Cow Lane also has a predominance of willow, and one might expect mean chick masses in Wicken Fen and Cow Lane to be similar. So why do Cow Lane and Wicken Fen differ in reproductive success? One possibility is that due to small sample sizes at Wicken Fen, with data only being available for two years as opposed to ten years and seven years for blue tits and great tits respectively at Cow Lane, Wicken Fen was not tested sufficiently. Also Wicken Fen has the added problem of heavy predation and if this was taken into consideration, fledging success at this site would be much lower.

However, those nests that did go on to survive predation appeared to have greater reproductive success, implying better foraging conditions, than at Cow Lane. Is Cow Lane more variable in vegetation or do structural differences exist, with Cow Lane being patchier and less densely packed than Wicken Fen? Further investigations, for example with the use of LiDAR to measure habitat structure (e.g Hinsley *et al*. 2008) need to be carried out to test differences that exist between these two habitats.

4.4.1.1 Timing of reproduction

In the CUBG, great tits laid earlier than at Cow Lane and in small woods whereas blue tits laid later than in large woods, but did not differ significantly in laying date from all other sites (Table 4.13). It is interesting that great tits laid earlier at the CUBG than in small woods and Cow Lane but with similar timing to Wicken Fen and large woods. Early laying in urban environments has also been reported for great tits by other authors (e.g. Chamberlain *et al*. 2009; Cowie and Hinsley 1987; Dhondt *et al*. 1984; Perrins 1979). It has been argued that early layers do better, having larger clutches and higher quality offspring that go on to survive to breed (Perrins and McCleery 1989; Wilkin *et al*. 2009) and that early laying is an indication of better quality habitat (Arriero *et al*. 2006; Belda *et al*. 1998). However, the CUBG is clearly not a high quality habitat for great tits so why do they breed earlier and why do blue tits breed later? It has been argued that tits use appropriate proximate cues such as bud burst and temperature (Blondel *et al*. 1991, 1993; Visser and Holleman 2010; Visser *et al*. 1998), day length (Perrins 1979) and first appearance of caterpillar prey (Belda *et al*. 1998; Perrins 1991) to ensure that they time their reproduction with the peak abundance of caterpillars (Blondel *et al*. 1991). In urban environments however, temperatures are often warmer, potentially causing an earlier budburst, and have increased light levels due to artificial light (Partecke *et al*. 2004), which may affect photoperiod. Both of these factors may

enhance laying (Chamberlain *et al*. 2009). Similarly, food supplementation experiments have demonstrated advanced laying dates in birds (Clamens and Isenmann 1989) and Chamberlain *et al.* (2009) argue that human provided food at bird tables in urban environments advance laying dates by improving body condition of adults. Food is also supplied at Wicken Fen, nearby to the nest boxes, to aid mist net capture. Great tits had similar laying dates at Wicken Fen compared to the CUBG, which would support this hypothesis. However, this doesn't explain why blue tits and great tits differ in their laying dates in the CUBG. One possibility is that great tits, being the more dominant of the species (Haftorn 1993) out-compete blue tits for food at feeders, but I think it unlikely that great tits would be able to completely exclude blue tits from feeders. It is also possible that the two species differ in their relative dependence/exploitation of food from feeders.

Another possibility for early laying in the CUBG is that great tits may be taking cues from inappropriate plants, such as exotics, that come into budburst earlier (Remeš 2003) and so inappropriately lay earlier. Hinsley *et al.* (2009) found that trees in urban parkland (and with a high tree species diversity) tended to leaf earlier than in woodland. Mistimed reproduction in great tits due to warmer temperatures advancing vegetation bud burst has also been record by Visser *et al.* (1998). Similarly, warmer temperatures can affect the caterpillar prey by creating a mismatch between bud burst and caterpillar hatching (Visser and Holleman 2010). Blue tits however, being more closely adapted to oak woodland (Perrins 1979) may be using more appropriate plants such as oaks and other native trees such as birches as budburst cues. In addition, if first appearance of caterpillar prey is associated with laying date (Belda *et al*. 1998; Perrins 1991) it could be possible that feeding on the caterpillars themselves produces a chemical reaction that instigates laying. Great tits were observed feeding more frequently than blue tits on

exotics with earlier bud burst (see Chapter 3) and thus their laying date may be advanced. All of the above are testable hypotheses that require further investigations.

Also surprising is that great tits at the CUBG had laying dates that did not differ significantly from Wicken Fen but had significantly earlier dates than at Cow Lane, indicating Wicken Fen was also earlier than Cow Lane. Cow Lane and Wicken Fen are similar habitats (superficially at least) so why would great tits lay earlier at Wicken Fen? Wicken Fen may represent a better quality habitat, as indicated by heavier chicks at this site than at Cow Lane. Another reason may be predation pressure. In the years studied, Wicken Fen suffered from high weasel predation and since some evidence has shown that an individual tit can learn when to lay through experience from the previous breeding season (Grieco *et al*. 2002; Gienapp and Visser 2006), great tits may have learned to lay early at Wicken Fen. Therefore if they lose their first attempt to predation they have time for a second attempt at breeding. Blue tits rarely have a second brood (Perrins 1979) and so this would not apply to them.

4.4.2 Habitat and reproductive success within the CUBG

Blue tits and great tits did not differ in their fledging success (proportion of eggs turned into fledglings) within the CUBG, suggesting that their reproductive performances are similar with regards to output. However, as mean mass is an indication of future survival, with heavier chicks being more likely to survive (e.g. Perrins 1965), these results suggest that blue tits perform better reproductively than great tits in the CUBG because their chicks may have better survival potential.

Within the CUBG, the habitat surrounding a nest box appeared to have more of an impact on blue tit reproductive success than on great tit success. For blue tits, larger

percentages of non-native trees and shrubs, gaps and evergreen trees and shrubs had negative effects on chick mass or brood biomass. In contrast, larger percentages of native trees and shrubs, deciduous trees and shrubs, oaks and birches had positive effects. For great tits however, the only variable to have a significant impact on reproductive performance was native trees and shrubs, where a greater percentage had a mainly positive effect on mean chick mass. This suggests that blue tits were affected by both structural and functional gaps whereas great tits were affected mainly by functional gaps.

The differences found agree with previous investigations that have found that blue tits are more specialist in their exploitation of trees than great tits (e.g. Török 1985; Lack 1955). Lack (1955) for example found blue tits were twice as numerous in rich broad-leaved woods as great tits and much scarcer in coniferous plantations. In the CUBG, great tits were affected by the percentage of native trees and shrubs whereas blue tits in addition to this were affected by the relative abundance of specific broad-leaved taxa (oaks and birches). If great tits are more generalist surely they would do better reproductively than blue tits, which appear to be more constrained to specific tree types? However, this might also be interpreted as blue tits being better able to exploit the resources offered by these tree species, resulting in higher quality chicks, with, by virtue of their greater mass, a higher likelihood of recruitment.

Great tits may therefore have other constraints that negatively affect their reproductive performance in the CUBG. For example great tits being the larger of the species feed their chicks larger prey items than blue tits (Perrins, 1979; Hinsley *et al*. 2008) and the availability of larger prey items may be lower in the CUBG, giving blue tits an advantage. Also, with individual tree species such as oaks being quite sparse and isolated in the CUBG and with few very mature trees and an abundance of shrubs, the

caterpillar prey is likely to be depleted much quicker than in woodland. Blue tits may be able to exploit more of this caterpillar prey as, by being more agile foragers (e.g. Suhonen *et al*. 1994**),** they may have greater access to more of the tree by exploiting the thinner twigs, which are fairly inaccessible to great tits (e.g. Hino *et al*. 2002) (this will be discussed more in Chapter 5).

Great tits have been shown to be highly selective for large caterpillar prey for their chicks and only switch to this prey type (from spiders) when the caterpillars reach a certain mass (heavier than spiders) (Naef-Daenzer and Keller 1999; Naef-Denzer *et al*. 2000). In these studies, nestling growth rate was shown to be significantly influenced by caterpillar mass (Naef-Denzer *et al*. 2000) and parents were shown to save 40% of searching effort when feeding their broods within the timing of the caterpillar peak (Naef-Daenzer and Keller 1999). Naef-Daenzer and Keller (1999) argue that when caterpillar prey availability is low, parents may not be able to provide enough food for the chicks and the parents would have to work harder to satisfy the brood. As these studies were conducted in oak woodland where caterpillars were plentiful, it is likely that in the heterogeneous landscape of the CUBG that prey availability is relatively poor and adults may struggle to provide enough chick food. Therefore if great tits in the CUBG also only switch to caterpillar prey when it reaches a certain mass, resources of this prey type may be quickly diminished forcing them to use other potentially lower quality prey. Increased search times and distances travelled in finding larger prey that may be sparse in the CUBG would also increase the cost to the parents in terms of reduced feeding rates for the chicks and increased energy expenditure for the adult (e.g. Hinsley *et al*. 2008) compared with blue tits. Blue tits may also significantly reduce the abundance of smaller caterpillar prey before it can reach the larger sizes required for the great tit chicks (Minot 1981; Minot and Perrins 1986), further reducing the availability of this preferred prey type for great tits.

In the CUBG, for the vast majority of the habitat variables effecting blue tit reproduction, interactions between habitat and year were common. Consequently, the relationship between the habitat type and reproductive performance was variable across years. In general, in 2003 and 2008 the significant habitat variables had either no relationship with reproductive performance or the opposite relationship. For example, chick biomass decreased as the percentage of evergreen trees and shrubs increased in all years apart from in 2003 and 2008 where the reverse of an increase was observed. In these years therefore other factors, especially certain weather conditions and their timing (Hinsley *et al.* 2006), may have had more of an impact on reproductive performance with the apparent 'opposite effect of variables' probably being coincidental. Blue tits for example in these two years laid quite late (mean first egg date for 2003 was 27th April and 26th April for 2008), which, in 2008, was probably due to very heavy rain in March (BBC 2008a) and April (BBC 2008b). This was further compounded by above average rainfall in May (BBC 2008c), coinciding with chick food demand. In 2003 heavy rain fall again affected East Anglia in mid May (BBC 2003). Other authors have also found poor weather to affect prey availability and reproductive performance between years (Cowie and Hinsley 1987; Hinsley *et al*. 2008; Lõhmus 2003). In the CUBG, poor conditions affecting caterpillar prey (cold weather, heavy rain etc) may make oaks and birches caterpillar poor, along with all other plants, compounding the effects of the poor habitat. Therefore the effect of the oaks and birches on chick weight and biomass would be negligible in years of poor weather in all habitat types. In good years however, oaks and birches may be caterpillar rich and so breeding success increases with their proximity.

This data set within the CUBG is not without its problems. Certain biases may have been present due to a small dataset testing the relationship between nest box and habitat.

Between 2003-2005, there were a lower number of boxes present in the CUBG and blue tits may have been out competed for these by great tits, meaning even lower box occupancy (for the blue tit tests the sample size was 6 nest boxes in 2003 and 2 nest boxes in 2004 and 2005). From 2006 onwards, with the introduction of more nest boxes and ones with blue tit only sized holes, the sample size did increase (maximum box number used in the tests was 14 in 2006 and 2007). It is also interesting that a relationship was found for great tits between nest box and the percentage of native trees and shrubs but not for nest box and percentage of non-native trees and shrubs. I would have expected these tests to have had similar results but with an inverse relationship. Again this could be due to a small dataset (for the great tit tests the sample was between 5 and 12 nest boxes across all years).

4.4.3 Conclusions

To summarise, this study indicated that reproductive success was poor at the CUBG in comparison to large woodlands and Wicken Fen and to a lesser extent poorer than at Cow Lane and in small woods. Despite both species reducing their clutch sizes in comparison to the other sites, their clutch sizes at the CUBG were maladaptive, as indicated by significantly lower brood biomasses. Both species were also unable to raise large broods with chicks with healthy masses and had high chick mortality (indicated by low biomass for large clutches) when they tried. This indicated a food-poor habitat. However, blue tits performed better than great tits at the CUBG, having higher quality chicks with greater mean masses and hence a greater likelihood of survival and recruitment. This may indicate greater adaptability to poor habitats than great tits.

Habitat and year interactions within the CUBG showed that habitat and reproductive relationships are complicated and other factors such as annual variation in

environmental conditions need to be taken into account. However, positive relationships between native trees and shrubs for both blue tits and great tits within the CUBG suggest that habitat in parks and gardens could be improved by increasing the proportion of native plant species. For blue tits reproductive performance was linked to specific native taxa (oaks and birches) and this result is likely to transfer to other leaf-gleaning bird species. However, the introduction of more specific taxa to parks and gardens would need to be carefully considered to ensure the needs of the majority of bird species inhabiting those areas were taken into account.

CHAPTER 5

Foraging behaviours and techniques by blue tits and great tits in the Cambridge University Botanic Garden during the breeding season

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5.1 Introduction

In oak woodland blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) have been shown to change their foraging behaviours throughout their year in accordance with food availability (Gibb 1954). In the breeding season this leads to both species being less segregated from each other in feeding habit, with great tits moving from ground feeding to the canopy to take advantage of the abundance of winter moth larvae for their nestlings (Hartley 1953; Lack 1971). Both, however, occupy distinct feeding niches and have evolved characteristic feeding techniques to allow co-existence. For example, blue tits feed higher up in the canopy than great tits and take prey from twigs rather than branches which are used more frequently by great tits (Gibb 1954; Lack 1971).

These differences have been attributed to a variety of factors. Morphologically, great tits are larger than blue tits and their beak shape differs, allowing them to take larger prey and break into harder seeds (Lack 1971). Being larger may also allow great tits to dominate smaller tit species for access to better foraging sites (Alatalo *et al*. 1987; Hino *et al*. 2002; Suhonen *et al*. 1994). Blue tits and other smaller tit species, being lighter, are more agile and able to hang glean, allowing them to exploit areas of a tree, such as the thin exterior twigs, that are relatively inaccessible to the larger tits (Hino *et al*. 2002; Suhonen *et al*. 1994). Hang gleaning is argued to be more energy expensive for larger tits (Hino *et al*. 2002; Park *et al*. 2008), which prefer to perch glean, and may result in

reduced foraging efficiency (Rytkönen and Krams 2003). Great tits are able to hang, but intraspecifically body mass is related to hanging performance, with lighter individuals spending more time hanging than heavier ones (Moreno *et al*. 1997). Additionally, the hind limb leg morphology of the blue tit and the shortness of its leg compared to other species of tits fit the mechanical requirements for hanging, more so than the leg morphology of the great tit (Moreno and Carrascal 1993).

Habitat structure has also been shown to affect foraging behaviours. Foraging techniques by individual birds for example may differ depending on the tree species they are foraging in (Hino *et al*. 2002; Holmes and Robinson 1981; Maurer and Whitmore 1981; Unno 2002; Whelan 2001). It has been argued that this is related to the differing foliage structures across the trees (Holmes and Robinson 1981; Unno 2002; Whelan 2001) and to the morphology of individual bird species (Park 2005; Unno, 2002). Some species of tree may therefore be unsuitable foraging sites for tits, not because they have a reduced abundance of suitable prey items, but because the foliage structure and morphology make foraging difficult. For example, in a Japanese deciduous forest great tits avoided using birch trees, preferring oaks instead, even though they had similar prey abundances, because the long thin twigs, long leaf stalks and horizontally distributed leaves of birch made perching (their preferred manoeuvre) difficult (Unno 2002). The most efficient technique therefore depended on the foliage structure of the tree. If foraging efficiency of tits in habitats is linked to tree species morphology, with different bird species evolved to exploit different kinds of trees, and the foliage within the trees, efficiently (Suhonen *et al*. 1994), how will foraging behaviour be affected if the habitat they occupy has a widely heterogeneous vegetation structure, with relatively low numbers of preferred trees?

The Cambridge University Botanic Garden (CUBG), a large urban park in the centre of Cambridge city, is an example of this kind of habitat structure. Here, tree and shrub species diversity are high and species composition is varied and heterogeneous. Breeding success of blue tits and great tits has been shown to be poor in comparison to woodland (Hinsley *et al*. 2008, 2009; Chapter 4). The aim of this chapter is to compare foraging behaviour throughout the breeding season both within and between blue tits and great tits in the CUBG and assess the implications that habitat structure may have on their ability to forage successfully (in the context of previous literature for woodland breeders).

5.2 Methods

Observations of foraging behaviour were conducted from late March to mid-June during the 2006-2008 breeding seasons at the CUBG (see Chapter 2 for site description). For each observation, the date, time and location were noted. To avoid biasing observations to any particular part of the CUBG, it was split into six sections and each section visited following a random rota. Birds were fitted with unique combinations of colour rings (see below, section *5.2.1*) to enable identification of individuals within the field. In 2008, a more intensive survey was conducted on blue tits feeding young in known nest boxes (see Chapter 3 methods section *3.2.3* for more details). The 2008 field season began as above, with the six sections being visited in a random sequence. Once it was known which boxes were being used by breeding blue tits, a 100m radius area around the focal box was defined and multiple observations of the parent birds were taken. The 100m radius areas around the boxes (a total of 14 blue tit boxes were occupied) were sampled equally in a random sequence. If a box failed (eggs didn't hatch, chicks died etc) the area was no longer observed. Once all blue tit chicks were known to have

fledged from the boxes, the method reverted back to taking observations within the six sections, since the birds were no longer confined to an area around a box.

5.2.1 Colour ringing

Colour ringing was conducted during the winter (Dec-Feb) and adult blue tits and great tits were caught in mist nets around an area baited with peanuts and within close proximity to nest boxes. Mist netting is a technique to catch birds in flight by using a fine mesh black net erected on and between two poles. Against a background from vegetation, the net is inconspicuous to the birds enabling capture in flight. Birds are unharmed by the netting and can be safely removed by British Trust for Ornithology (BTO) trained ringers. Once removed from the net, birds were placed in a bag and processed as soon as possible after capture to prevent undue stress. Processing involved placing a lightweight BTO aluminium ring, each uniquely numbered, on the right leg and either two colour rings on the left leg or one colour ring over the BTO ring and another colour ring on the left leg. Colour ring combinations were used only once for each species to enable individuals to be identified. Following Svensson (1992) the weight (using a Pesola or Salter spring balance to the nearest 0.1g), wing measurement (max chord of wing measured on a stopped ruler), age (first year or older) and sex (blue tits only in the breeding season by brood patch/cloacal protuberance) were recorded before the bird was released near to the point of capture. Any breeding adults not ringed in the winter were caught using a trap in the box when nestlings were at least 8 days old (to avoid nest desertion). They were then ringed and processed as above before being returned to the box.

5.2.2 Bird observations

An individual bird was located (by sound and/or visually using 8 x 42 binoculars) and its species, identity (colour ring combination) and foraging behaviour were recorded, along with the time and date of location and the section of the CUBG where it was found. It was noted if the focal bird was with another adult or fledgling(s), the latter defined as being within approximately 5 m of the focal bird and actively communicating, i.e. feeding the focal bird, or being fed by it and/or calling. If the focal bird was with another colour-marked foraging adult the behaviour of the second bird was recorded as a separate observation. Observation bouts of individuals lasted for as long as the bird was in sight or for a maximum of 5 min if the bird did not move from the foraging site. Consecutive records were taken if the bird moved from one foraging site to another or from a nest box/fledgling location back to the same or a different foraging site. If the same foraging site was visited consecutively, the frequency of visits was recorded.

Any of the following foraging behaviours seen in an observation bout were noted:

ii. Gleaning – actively feeding, picking small items from leaves or branches. This category included hover-gleaning where the bird is behaving as described but is in flight
iii. Searching - actively looking for food but not picking up or feeding on an item
iv. Probing - taking prey from an opening e.g. flower or bark crevice
v. Prey handling - rubbing and or hitting the prey item, usually on a branch
vi. Other – any other foraging behaviour not mentioned above

Any of the following foraging positions seen in an observation bout were noted:

i. Hanging – gripping with feet to suspend the body below the feet (see Remsen and Robinson 1990 for a more detailed explanation)

ii. Standing – positioned upright, supported by the feet and legs. Walking/hopping in an upright position is also classed as standing

iii. Other – any other foraging position not mentioned above such as hovering

5.2.3 Habitat details

The species of plant in which the observed individual was found foraging was noted along with the variables listed below. For these variables, as the bird was moving during a foraging bout, the height, location and substrate categories could change. In these cases, multiple categories within each variable could be recorded per observation.

iv. Foraging height – three height categories: 0 to 1m, >1 to 3m and/or >3m (estimated in the field)

v. Foraging location – six location categories: trunk, branch (> 1cm diameter), twig (< 1cm diameter), herbaceous layer (any ground-covering native plants such as cow parsley (*Anthriscus sylvestris*) or ivy (*Hedera helix*) but not lawn), ground and/or other (anything else not categorised)

vi. Foraging substrate (where the bird actually searched or obtained food from) – eight substrate categories: bark, bud, emerging leaf, full leaf, emerging flower, full flower, fruit and/or other (anything else not categorised)

5.2.4 Statistical analyses

Frequency tests were carried out using all foraging observations from 2006-2008 of both blue tits and great tits. One-way chi-square goodness-of-fit tests and two-way G-

tests (likelihood ratio tests) were used to test for non-random foraging behaviour of blue tits and great tits separately in the CUBG. For the one-way tests, those observations in which multiple foraging categories within a variable had been recorded were excluded. So, for example, only observations where a bird used foraging height >3m or used foraging substrate full leaf, and no other foraging height or substrate, were included. This did mean than N varied between tests and also within the six repeated tests (using different random numbers – see below for explanation) because foraging observations that had included records of more than one category within a variable were not used. However, it gave more opportunity to test for patterns using each variable type.

Two-way G-tests were used to analyse the individual foraging categories (height, location, substrate) to see if foraging differed between breeding periods (period one - nest building, egg laying and incubation, period two - chick feeding and period three – fledging, when the adults were seen with their young foraging outside of the box) and between specific tree genera (*Acer, Betula, Prunus and Quercus*) within the two bird species. Two-way G-tests also analysed differences between the bird species in their use of the individual foraging categories.

In these tests, only one observation of an individual bird was used to prevent pseudoreplication (resulting from repeated observations of the same individual). The observation of each individual of each species was chosen using the random number selection outlined in Chapter 3 (methods section *3.2.3.1*) where the data were sorted by species and then by individual (by their colour rings) and then the first observation from the lowest random number was selected for the analyses to test foraging behaviour. A separate random number category was generated to analyse foraging behaviour across four of the more frequently used tree/shrub genera (*Acer, Betula, Prunus and Quercus*) and for these analyses, data were sorted in Microsoft Office Excel version 10 (Microsoft

Corporation 1985-2001) by bird species, then by the four selected genera then by individual and then again each observation of an individual from the lowest random number was selected. In this way the probability of a bird feeding on plants of the chosen genera could be analysed, using data only for observations of individuals feeding on those specific plants.

To improve the reliability of each test, since the chosen observation of a specific individual may not have been representative of its usual behaviour, the tests were repeated six times using different observations chosen by six different random numbers. The numbers of significant tests out of the six were tabulated. Test values and significance levels were only reported for two of the tests, those having the highest P value (or lowest chi-square/G-test value) and those having the lowest P value (or highest chi-square/G-test value).

All frequency tests were performed in SPSS 16.0 for Windows (SPSS Inc 2007), and reported the Monte Carlo significance value or the Exact significance value (when Monte Carlo was not available) due to some of the data being unbalanced and some tests reporting expected frequencies of less than five. The Monte Carlo and Exact methods calculate a more accurate significance level than the SPSS default, asymptotic calculation.

5.3 Results

5.3.1 Blue tit foraging

Table 5.1 summarises blue tit foraging in the CUBG and shows all 6 of the repeated tests being significant for foraging height, foraging location, foraging substrate and

foraging behaviour. Figures 5.1 and 5.2a outline the patterns of these significant tests with blue tits using the foraging height '>3m' most frequently, more than expected by chance, and '0 to 1m' relatively infrequently, less than expected by chance (Figure 5.1a). Blue tits used the foraging location 'twig' most frequently, significantly more than expected by chance and all other categories less than expected by chance (Figure 5.1b). Blue tits used the foraging substrate 'full leaf' most frequently, significantly more than expected, and to a lesser extent used 'flowers' more than expected by chance (Figure 5.1c). Finally, blue tits used the foraging behaviour 'gleaning' most frequently, more than expected and used 'searching' and 'probing' less than expected by chance (Figure 5.2a).

There was a tendency for blue tits to forage alone more frequently than with another adult (Figure 5.2b), but with three out of the six tests being significant this remains inconclusive (Table 5.1d). Blue tits showed little difference in their use of foraging positions (Table 5.1f) and were found to 'stand' and 'hang' equally (the category 'other' was not included in the test, being recorded very infrequently).

5.3.1.1 Blue tit foraging between breeding periods

Table 5.2 outlines the results of the tests analysing blue tit foraging in the different breeding periods and shows significant results, with all six repeated tests being significant, for the foraging substrates 'full leaf' and 'full flower' (Table 5.2f and g) and significant results for 'foraging alone' (Table 5.2l), with four out of the six tests being significant. Figure 5.3 shows the pattern of these significant results with blue tits using the foraging substrate 'full flower' most frequently, more than expected by chance in the nest building/egg laying/incubation period (Figure 5.3a) whereas they used the foraging substrate 'full leaf' most frequently, more than expected by chance in the chick

feeding and fledging periods (Figure 5.3b). Blue tits 'foraged alone' most frequently, more than expected by chance in the chick feeding period and less than expected by chance in the fledging period (Figure 5.3c). They also 'foraged with an adult' less than expected by chance in the fledging period (Figure 5.4a), although the results from these tests showed only three out of the six to be significant and hence are relatively inconclusive (Table 5.2m). However, since adult birds foraged less frequently alone and also less frequently with an adult in the fledging period this would indicate that single adults were foraging with fledglings more frequently than paired adults with fledglings.

Three out of the six tests being significant for foraging on the substrate 'bark' and for 'searching' behaviour indicated a tendency for differences between the breeding periods, although not conclusively. Figure 5.4b indicates that 'bark' was used most frequently, more than expected by chance in the nest building/egg laying/incubation period and used less than expected by chance in the other two periods. Figure 5.4c indicates that blue tits 'searched' more frequently, more than expected by chance in the chick feeding and fledging periods.

Blue tits did not differ in their use of the foraging heights '>1m to 3m' and '>3m', the foraging locations 'branch' and 'twig', the foraging behaviour 'glean' and the foraging positions 'stand' and 'hang' (Table 5.2). This indicated equal use of all these categories across the breeding periods.

5.3.1.2 Blue tit foraging between genera

Table 5.3 summarises the results from the tests analysing blue tit foraging on four genera of trees. Only the results for use of the substrate 'full flower' showed differences between genera, with four out of the six tests being significant. Figure 5.5 shows that

blue tits foraged most frequently and more than expected by chance on the 'full flowers' of *Betula* and to a lesser extent *Prunus* and less than expected by chance on the 'full flowers' of *Acer* and *Quercus*.

Two of the six tests being significant for the foraging substrate 'full leaf', the behaviour 'glean' and the foraging position 'hang' (Table 5.3d, f and i) may indicate a pattern showing weak differences between genera with a tendency 1) to use the leaves of *Acer* and *Prunus* more than expected by chance and the leaves of *Betula* and *Quercus* less than expected by chance (Figure 5.6a), 2) to use the behaviour 'glean' more than expected by chance on *Betula* and less than expected by chance on *Quercus* (Figure 5.6b) and 3) to use the foraging position 'hang' more than expected by chance on *Betula* and less than expected by chance on *Acer* and *Prunus* (Figure 5.6c). However, these results remain inconclusive. With the sample for all of these tests being split between the four genera, the sample sizes may not have been large enough for the tests to be able to pick up patterns. One example of this is the behaviour 'search', where although only one of the six tests was significant, two more were nearing significance ($P<0.08$). Figure 5.7 indicates that blue tits 'searched' more than expected by chance on *Quercus* and less than expected on *Acer* and *Betula*. Blue tits were found to use the foraging locations 'branches' and 'twigs', the substrate 'bark' and the foraging position 'stand' equally on all genera types (Table 5.3a, b, c and h).

Table 5.1 Chi-square goodness-of-fit tests comparing observed and expected frequencies of use of various foraging variables by blue tits. The table shows the result of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. N varies between test variables and between the repeated tests due to the selection of only one foraging category within a variable (see methods for a more detailed explanation).

	Test	Number of tests which are significant (out of 6)	*df*	χ^2 test of highest P value		χ^2 test of lowest P value	
				χ^2	*N*	χ^2	*N*
a)	Foraging height	6/6	2	50.000***	93	79.753***	97
b)	Foraging location	6/6	3	107.076***	79	168.862***	87
c)	Foraging substrate	6/6	4	35.125***	80	95.865***	74
d)	Foraging associations (alone or with an adult)	3/6	1	2.279	86	11.378***	90
e)	Foraging behaviour	6/6	2	32.986***	71	65.158***	76
f)	Foraging position	1/6	1	0.023	43	6.811*	53

Table 5.2 Two-way G-tests (likelihood ratio test) comparing breeding period (1. nest building/egg laying/incubation, 2. chick feeding and 3. fledging) against the observed and expected frequencies of blue tit use of various foraging categories. The table shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. N varies between some of the repeated tests due to missing data from some of the individual observations.

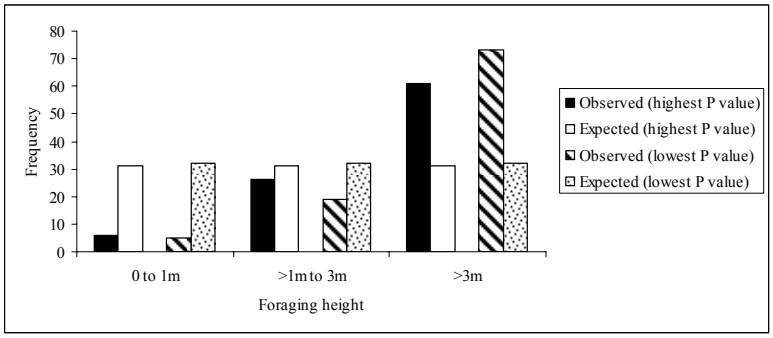
	Test	Number of tests which are significant (out of 6)	*df*	X^2 test of highest P value		X^2 test of lowest P value	
				X^2	*N*	X^2	*N*
	Breeding period by:						
a)	Height '>1m to 3m'	0/6	2	0.343	101	3.595	101
b)	Height '>3m'	1/6	2	0.254	101	6.284*	101
c)	Location 'branch'	1/6	2	0.229	101	8.834**	101
d)	Location 'twig'	0/6	2	0.806	101	3.978	101
e)	Substrate 'bark'	3/6	2	2.144	101	10.240**	101
f)	Substrate 'full leaf'	6/6	2	26.295***	100	49.314***	101
g)	Substrate 'full flower'	6/6	2	9.872*	101	18.233***	101
h)	Behaviour 'glean'	0/6	2	0.102	101	5.754	101
i)	Behaviour 'search'	3/6	2	0.094	101	13.174**	101
j)	Position 'stand'	1/6	2	2.491	93	9.315*	89
k)	Position 'hang'	0/6	2	0.116	89	1.826	92
l)	'Foraging alone'	4/6	2	0.772	101	18.215***	101
m)	'Foraging with an adult'	3/6	2	0.592	101	14.636***	101

Table 5.3 Two-way G-tests (likelihood ratio test) comparing four genera (*Acer, Betula, Prunus* and *Quercus*) against the observed and expected frequencies of blue tit use of various foraging categories. The table shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. N varies between some of the repeated tests due to missing data from some of the individual observations.

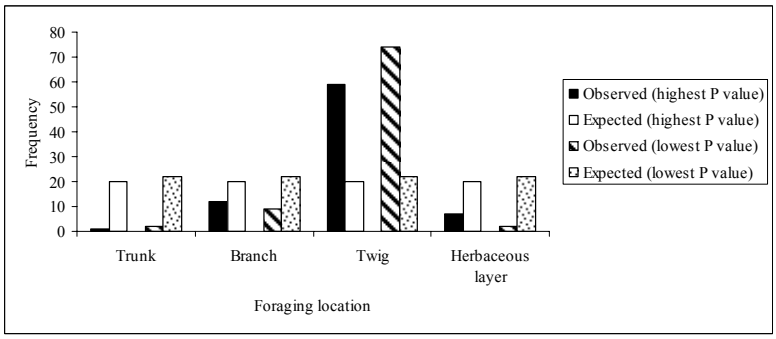
	Test	Number of tests which are significant (out of 6)	*df*	X^2 test of highest P value		X^2 test of lowest P value	
				X^2	*N*	X^2	*N*
	Genus by:						
a)	Location 'branch'	0/6	3	1.870	84	5.901	84
b)	Location 'twig'	1/6	3	0.598	84	8.709*	84
c)	Substrate 'bark'	0/6	3	0.300	84	4.453	84
d)	Substrate 'full leaf'	2/6	3	3.469	84	10.141*	84
e)	Substrate 'full flower'	4/6	3	2.789	84	14.337**	84
f)	Behaviour 'glean'	2/6	3	0.311	84	14.279**	84
g)	Behaviour 'search'	1/6	3	1.014	84	15.326**	84
h)	Position 'stand'	0/6	3	2.812	76	7.249	75
i)	Position 'hang'	2/6	3	1.045	76	9.499*	76

Figure 5.1 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit frequency of use of different a) foraging heights, b) foraging locations and c) foraging substrates. Missing categories within variables ('ground' and 'other' from foraging location and 'fruit' and 'other' from foraging substrate) are due to zero observations of these categories being generated from the random number selection for the majority of the six repeated tests. 'Full flower' and 'emerging flower' categories were combined for foraging substrate due to only one of the random number categories having zero observations for 'emerging flower'. The figure shows the results of the highest and lowest P values obtained from 6 repeated tests, with each test using an individual bird selected by a different random number. See Table 5.1a-c for the significance levels of these P values.

a) Foraging height



b) Foraging location



c) Foraging substrate

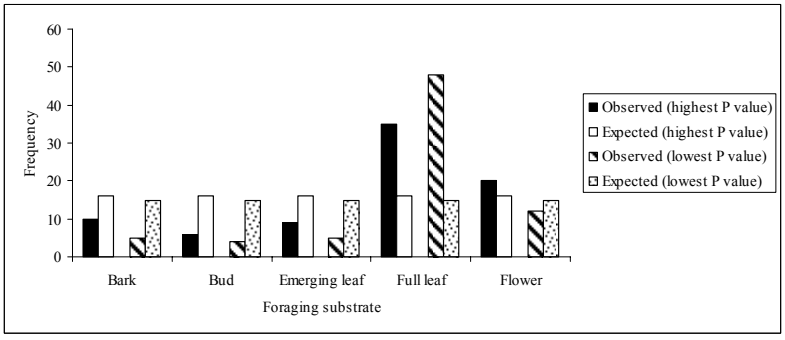
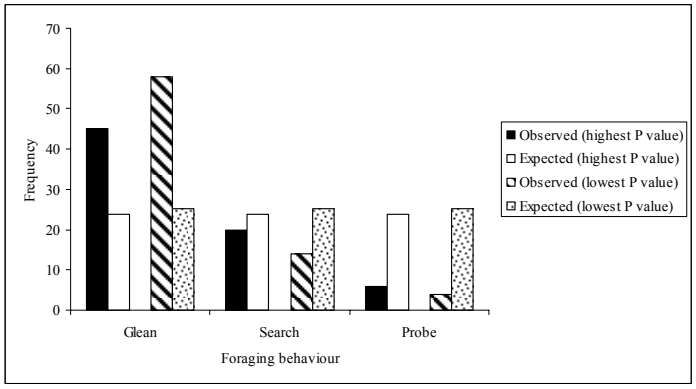


Figure 5.2 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing blue tit a) frequency of use of different foraging behaviours and b) frequency of foraging alone or in association with an adult. Missing categories within variables ('prey handling' and 'other' from foraging behaviour) are due to zero observations of these categories being generated from the random number selection for the majority of the six repeated tests. The figure shows the results of the highest and lowest P values obtained from 6 repeated tests, with each test using an individual bird selected by a different random number. See Table 5.1d (foraging associations) and 5.1e (foraging behaviour) for the significance levels of these P values.

a) Foraging behaviour



b) Foraging associations

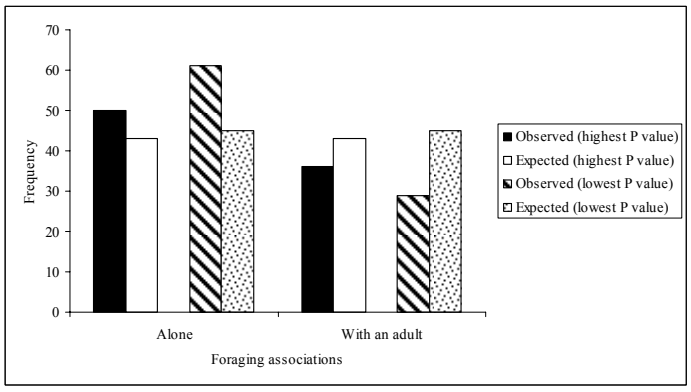
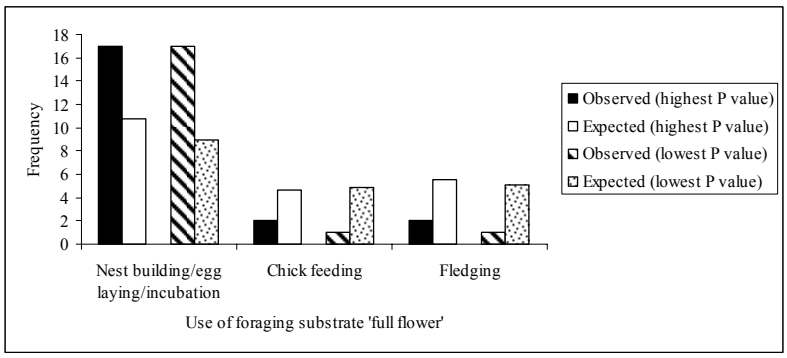
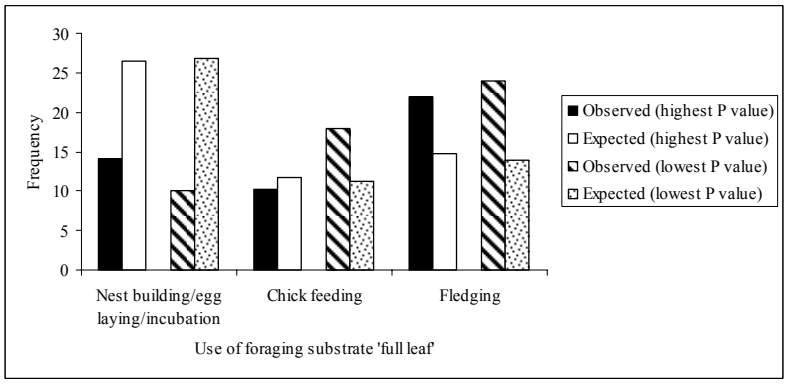


Figure 5.3 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing breeding period (1. nest building/egg laying/incubation, 2. chick feeding and 3. fledging) against blue tit use of the foraging categories ‘full flower’, ‘full leaf’ and ‘foraging alone’. The frequency of non-use of the categories, which was used in the test to generate the expected values, has been omitted from the graphs for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.2g (‘full flower’), 5.1f (‘full leaf’) and 5.2l (‘foraging alone’) for the significance levels of these P values.

a) Use of foraging substrate ‘full flower’



b) Use of foraging substrate ‘full leaf’



c) Use of category ‘foraging alone’

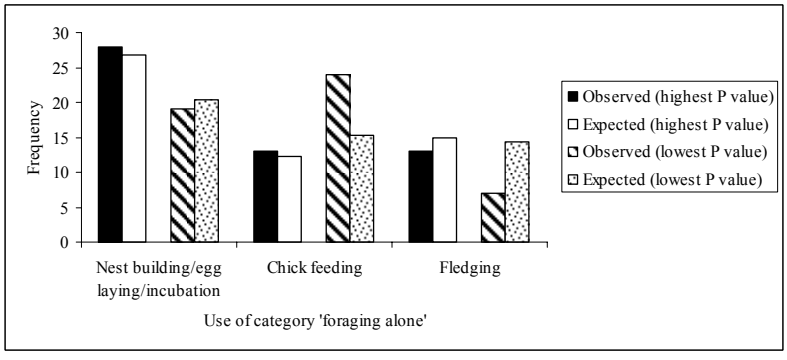
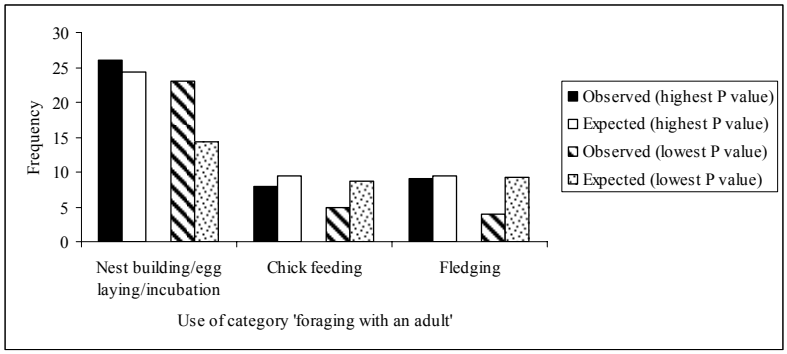
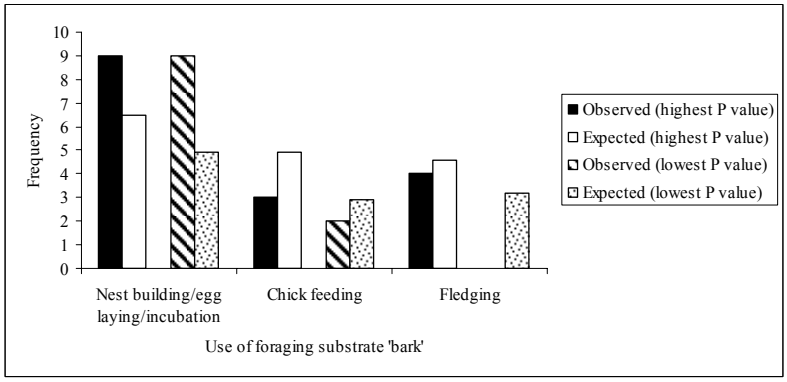


Figure 5.4 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing breeding period (1. nest building/egg laying/incubation, 2. chick feeding and 3. fledging) against blue tit use of the foraging categories 'foraging with an adult', 'bark' and 'search'. The frequency of non-use of the categories, which was used in the test to generate the expected values, has been omitted from the graphs for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.2e ('bark'), 5.2i ('search') and 5.2m ('foraging with an adult') for the significance levels of these P values.

a) Use of category 'foraging with an adult'



b) Use of foraging substrate 'bark'



c) Use of foraging behaviour 'search'

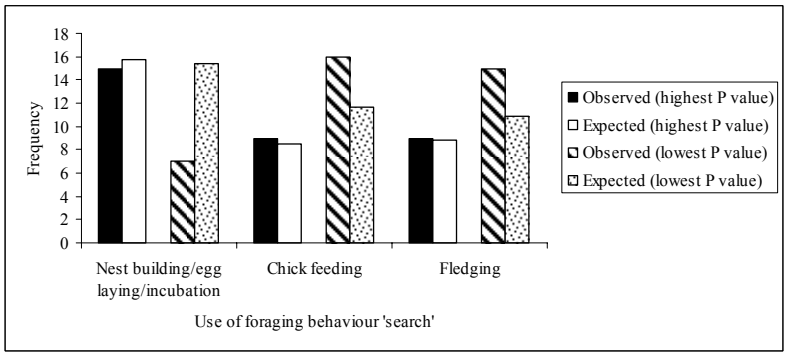


Figure 5.5 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing four genera (*Acer*, *Betula*, *Prunus* and *Quercus*) against blue tit use of the foraging category 'full flower'. The frequency of non-use of the category, which was used in the test to generate the expected values, has been omitted from the graph for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.3e for the significance levels of these P values.

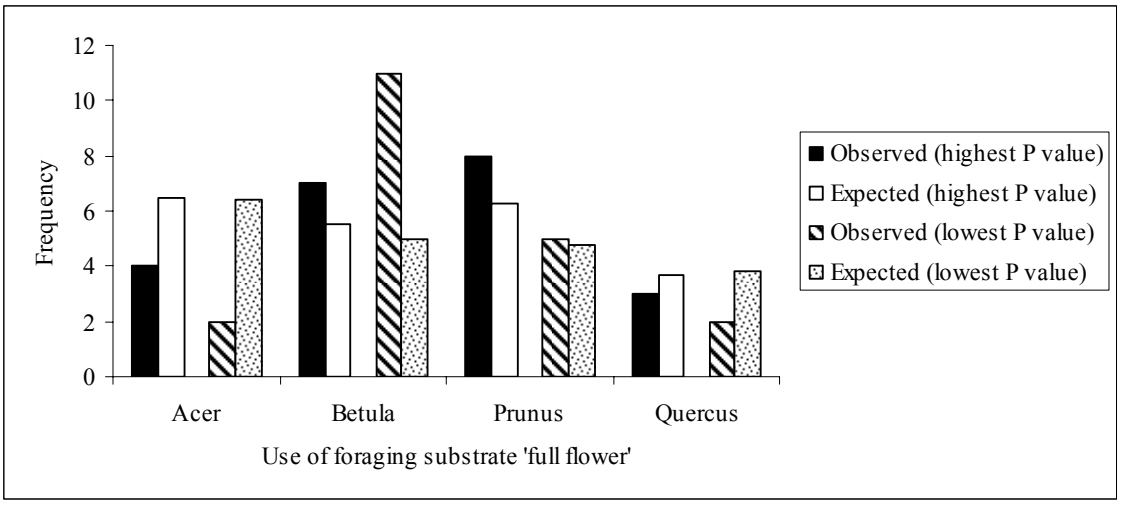
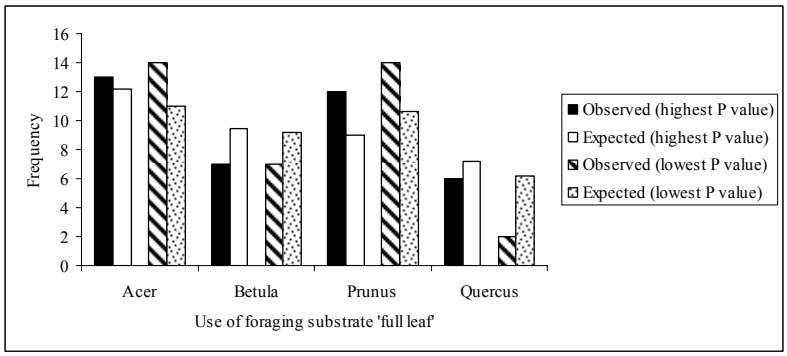
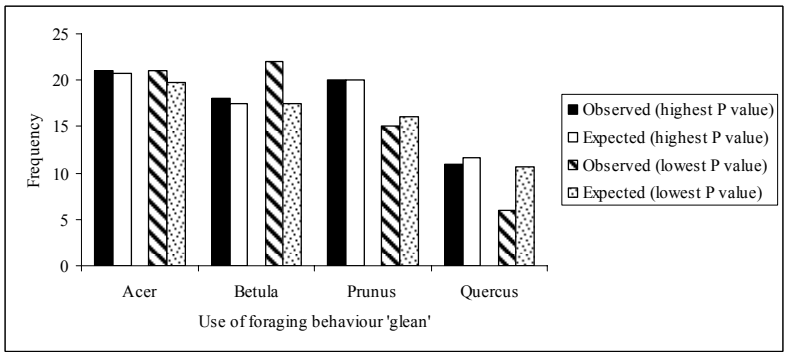


Figure 5.6 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing four genera (*Acer*, *Betula*, *Prunus* and *Quercus*) against blue tit use of the foraging categories 'full leaf', 'glean' and 'hang'. The frequency of non-use of the categories, which was used in the test to generate the expected values, has been omitted from the graphs for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.3d ('full leaf'), 5.3f ('glean') and 5.3i ('hang') for the significance levels of these P values.

a) Use of foraging substrate 'full leaf'



b) Use of foraging behaviour 'glean'



c) Use of foraging position 'hang'

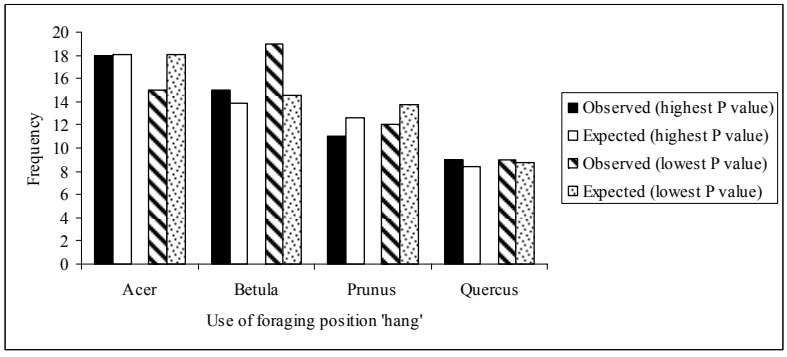
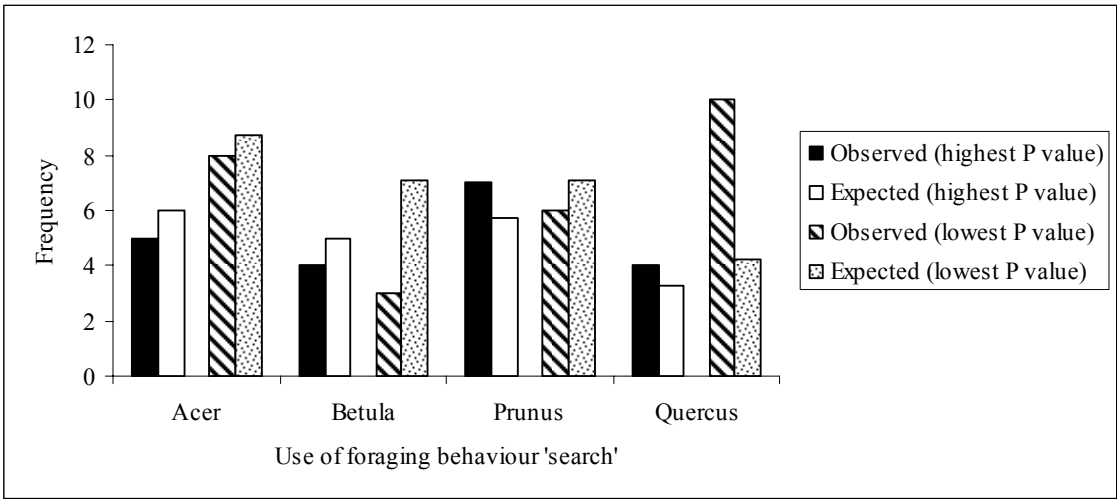


Figure 5.7 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing four genera (*Acer*, *Betula*, *Prunus* and *Quercus*) against blue tit use of the foraging category 'search'. The frequency of non-use of the category, which was used in the test to generate the expected values, has been omitted from the graph for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.3g for the significance levels of these P values.



5.3.2 Great tit foraging

Table 5.4 summarises great tit foraging in the CUBG within variables and shows all six of the repeated tests being significant for foraging location (Table 5.4b), foraging substrate (Table 5.4d), foraging behaviour (Table 5.4f) and foraging position (Table 5.4g) and four out of six of the tests being significant for foraging height (Table 5.4a). Figures 5.8 and 5.9 outline the patterns of these significant tests with great tits using the foraging locations 'twigs' and 'branches' most frequently, more than expected by chance, and all other categories being used less than expected by chance (Figure 5.8a). Great tits used the foraging substrate 'full leaf' most frequently, more than expected by chance and all other categories less than expected by chance (Figure 5.8b). They used the foraging behaviour 'search' most frequently, more than expected by chance (Figure 5.9a). The foraging position 'stand' was used more frequently than expected by chance with 'hanging' and 'other' positions being used very infrequently and less than expected by chance (Figure 5.9b). Finally, great tits used the foraging height '>3m' most frequently, more than expected by chance and the foraging heights '0-1m' and '>1m to 3m' were used less than expected by chance (Figure 5.9c). When only looking at 'twigs' and 'branches' as foraging locations, great tits were found to use both equally (Table 5.4c). They were also found to forage equally with an adult or alone (Table 5.4e).

5.3.2.1 Great tit foraging between breeding periods

Table 5.5 outlines the results of the tests analysing great tit foraging in the different breeding periods and shows significant results, with all six repeated tests being significant for the foraging substrate 'full leaf' (Table 5.5h). Figure 5.10 shows the pattern of these significant results with 'full leaves' used most frequently, more than

expected by chance in the fledging and to a lesser extent in the chick feeding periods, and less than expected by chance in the nest building/egg laying/incubation period.

With three out of the six tests for foraging with an adult being significant (Table 5.5n), although not conclusive, this indicated differences between the breeding period. Figure 5.11 outlines these differences with great tits foraging with an adult more than expected by chance in the nest building/egg laying/incubation period and less than expected by chance in the fledging period. There was relatively little difference between observed and expected values in the chick feeding period. Great tits did not differ in their use across breeding periods of the different foraging heights '0 to 1m', '>1m to 3m' and '>3m', the foraging locations 'branch', 'twig' and 'herbaceous layer', the foraging substrate 'bark', the foraging behaviours 'glean' and 'search', the foraging positions 'stand' and 'hang' and whether they were found 'foraging alone' (Table 5.5).

5.3.2.2 Great tit foraging between genera

Table 5.6 summarises the results from the tests analysing great tit foraging between three genera types (*Quercus* was not included due to a small number of observations). Only the results from their use of the substrate 'full leaf' indicated any differences between genera, with three out of the six tests being significant. Figure 5.12 outlines these differences and shows that great tits foraged most frequently and more than expected by chance on the 'full leaves' of *Prunus* and less than expected by chance on the 'full leaves' of *Acer*. Great tits were found to use the foraging locations 'branches' and 'twigs', the substrates 'bark' and 'full flower', the foraging behaviours 'glean' and 'search' and the foraging positions 'stand' and 'hang' equally on all genera types (Table 5.6a-c and e-i).

Table 5.4 Chi-square goodness-of-fit tests comparing observed and expected frequencies of use of various foraging variables by great tits. The table shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. N varies between tests and within the repeated tests due to the selection of only one foraging category within a variable (see methods for a more detailed explanation).

	Test	Number of tests which are significant (out of 6)	*df*	χ^2 test of highest P value		χ^2 test of lowest P value	
				χ^2	*N*	χ^2	*N*
a)	Foraging height	4/6	2	1.778	54	19.276***	58
b)	Foraging location	6/6	5	31.000***	51	42.855***	55
c)	Foraging location (branch and twig only)	0/6	1	0.029	35	3.600	40
d)	Foraging substrate	6/6	4	36.408***	49	98.800***	50
e)	Foraging assosciations (alone or with an adult)	0/6	1	0.022	45	4.261	46
f)	Foraging behaviour	6/6	3	26.182***	44	48.783***	46
g)	Foraging position	6/6	2	44.698***	43	76.894***	47

Table 5.5 Two-way G-tests (likelihood ratio test) comparing breeding period (1. nest building/egg laying/incubation, 2. chick feeding and 3. fledging) against the observed and expected frequencies of great tit use of various foraging categories. The table shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. N varies between some of the repeated tests due to missing data from some of the individual observations.

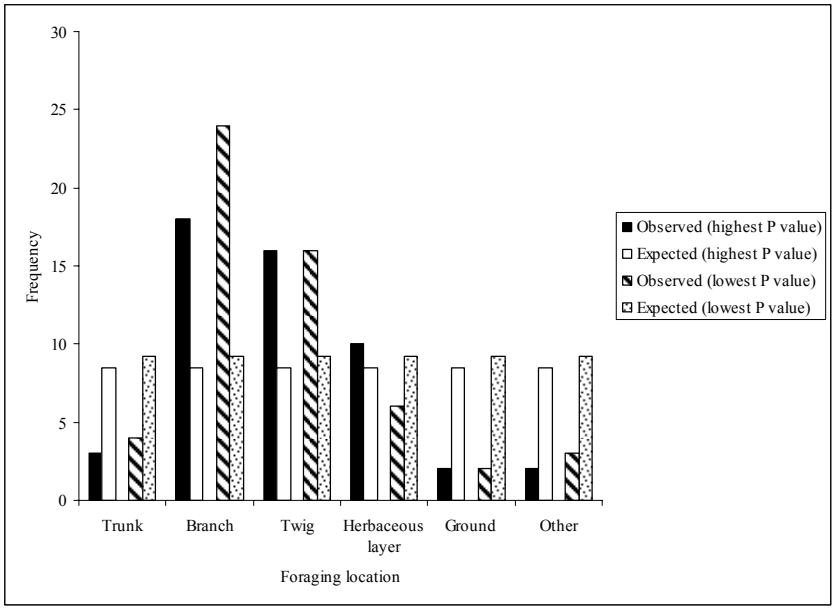
Test	Number of tests which are significant (out of 6)	*df*	X^2 test of highest P value		X^2 test of lowest P value	
			X^2	*N*	X^2	*N*
Breeding period by:						
a) Height '0 to 1m'	0/6	2	0.248	59	6.681	59
b) Height '>1m to 3m'	1/6	2	0.465	59	6.644*	59
c) Height '>3m'	0/6	2	1.114	59	7.273	59
d) Location 'branch'	0/6	2	0.082	59	1.703	59
e) Location 'twig'	0/6	2	0.057	59	4.901	59
f) Location 'herbaceous layer'	0/6	2	0.855	58	3.511	59
g) Substrate 'bark'	0/6	2	0.649	58	4.936	56
h) Substrate 'full leaf'	6/6	2	6.745*	57	11.553**	58
i) Behaviour 'glean'	1/6	2	0.769	59	6.634*	58
j) Behaviour 'search'	0/6	2	0.245	59	3.244	58
k) Position 'stand'	0/6	2	0.218	53	2.799	54
l) Position 'hang'	0/6	2	0.195	53	5.740	54
m) 'Foraging alone'	1/6	2	0.146	59	7.194*	59
n) 'Foraging with an adult'	3/6	2	1.358	59	9.259**	59

Table 5.6 Two-way G-tests (likelihood ratio test) comparing genera of three plants (Acer, *Betula* and *Prunus*) against the observed and expected frequencies of great tit use of various foraging categories. The table shows the result of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. N varies between some of the repeated tests due to missing data from some of the individual observations.

Test	Number of tests which are significant (out of 6)	*df*	X^2 test of highest P value		X^2 test of lowest P value	
			X^2	*N*	X^2	*N*
Genus by:						
a) Location 'branch'	0/6	2	1.079	37	5.486	37
b) Location 'twig'	0/6	2	1.394	36	3.356	36
c) Substrate 'bark'	0/6	2	1.932	36	5.641	35
d) Substrate 'full leaf'	3/6	2	3.453	35	10.172**	36
e) Substrate 'full flower'	0/6	2	0.032	35	4.897	35
f) Behaviour 'glean'	1/6	2	1.209	35	7.037*	37
g) Behaviour 'search'	1/6	2	4.654	36	7.197*	37
h) Position 'stand'	0/6	2	0.147	30	2.334	31
i) Position 'hang'	0/6	2	0.091	30	3.420	31

Figure 5.8 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing great tit frequency of use of different a) foraging locations and b) foraging substrates. Missing categories within variables ('bud', 'emerging flower' and 'fruit' from foraging substrate) are due to zero observations of these categories being generated from the random number selection for the majority of the six repeated tests. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.4b ('foraging location') and 5.1d ('foraging substrate') for the significance levels of these P values.

a) Foraging location



b) Foraging substrate

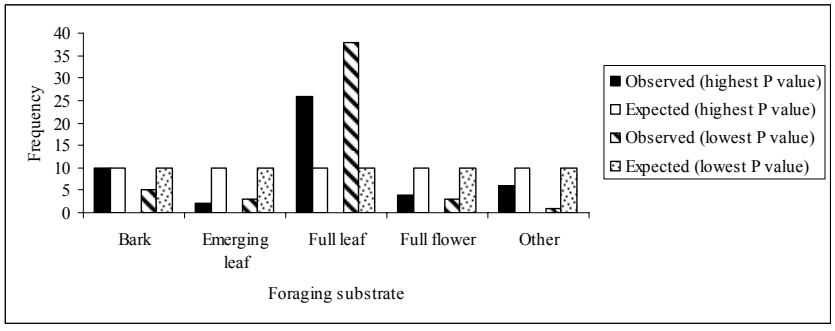
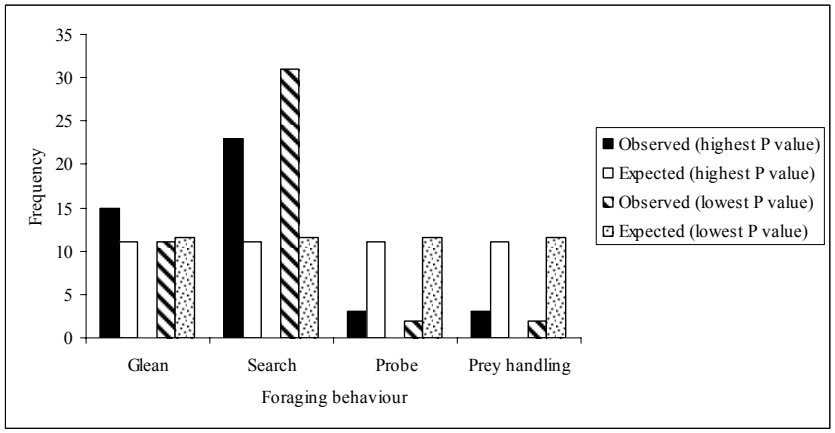
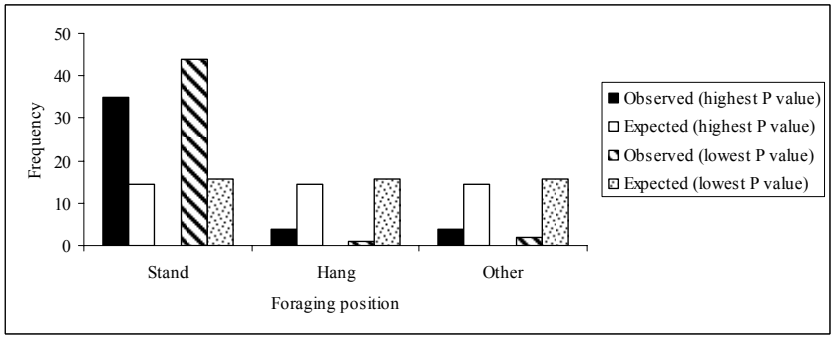


Figure 5.9 Observed and expected frequencies generated from chi-square goodness-of-fit tests showing great tit frequency of use of different a) foraging behaviours, b) foraging positions and c) foraging heights. The missing category 'other' from the foraging behaviour variable is due to zero observations of this category being generated from the random number selection for the majority of the six repeated tests. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.4a ('foraging height'), 5.4f ('foraging behaviour') and 5.4g ('foraging position') for the significance levels of these P values.

a) Foraging behaviour



b) Foraging position



c) Foraging height

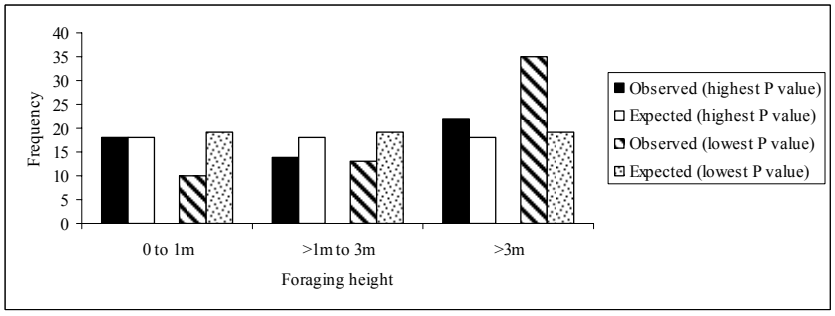


Figure 5.10 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing breeding period (1. nest building/egg laying/incubation, 2. chick feeding and 3. fledging) against great tit use of the foraging category 'full leaf'. The frequency of non-use of the category, which was used in the test to generate the expected values, has been omitted from the graphs for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.5h for the significance levels of these P values.

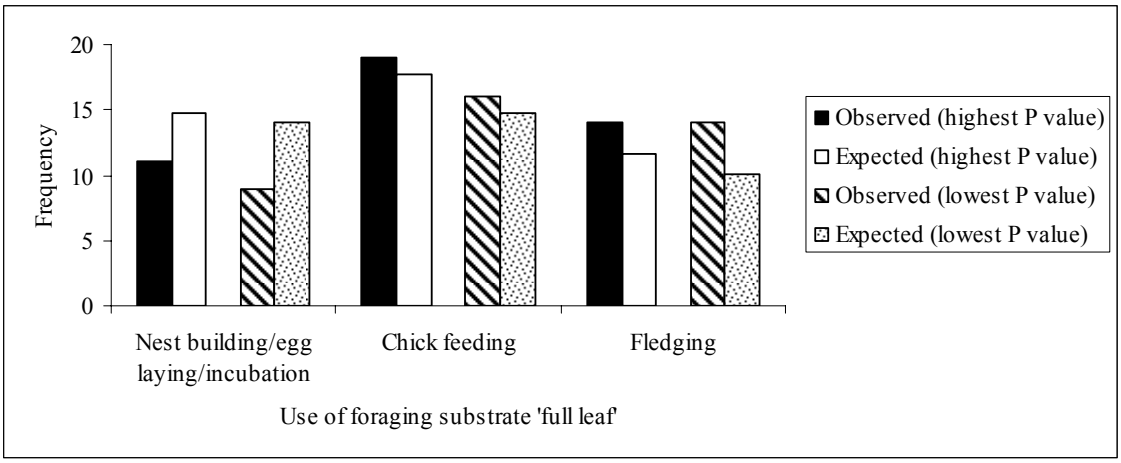


Figure 5.11 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing breeding period (1. nest building/egg laying/incubation, 2. chick feeding and 3. fledging) against great tit use of the foraging category 'foraging with an adult'. The frequency of non-use of the category, which was used in the test to generate the expected values, has been omitted from the graph for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.5n for the significance levels of these P values.

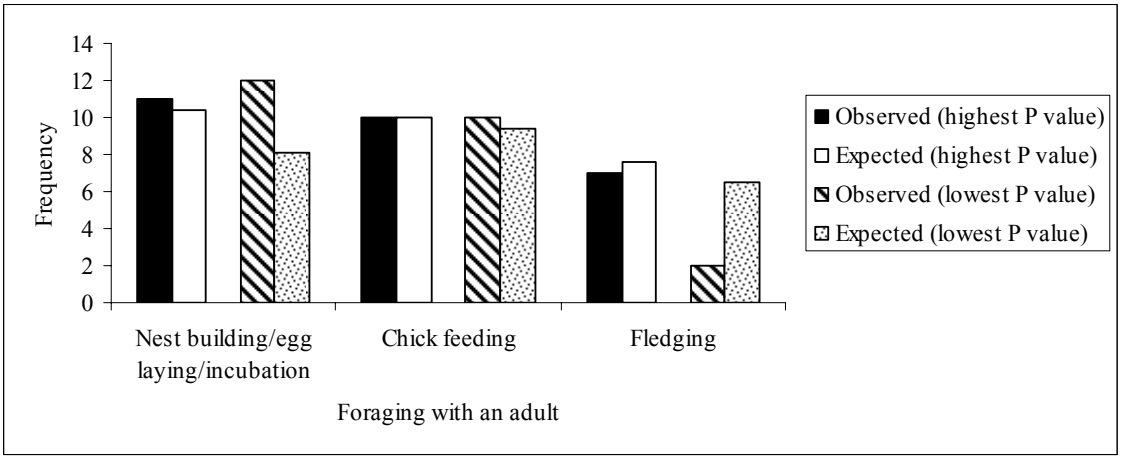
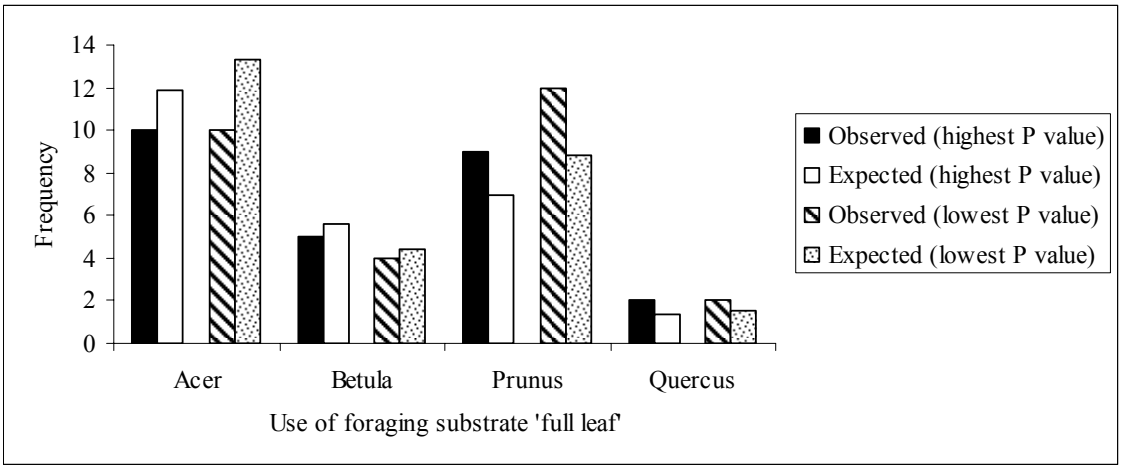


Figure 5.12 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing three genera (*Acer*, *Betula* and *Prunus*) against great tit use of the foraging category 'full leaf'. The frequency of non-use of the category, which was used in the test to generate the expected values, has been omitted from the graph for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.6d for the significance levels of these P values.



5.3.3 Comparisons between species

Table 5.7 outlines the results of the statistical tests comparing foraging between the two bird species and shows that blue tits and great tits differed significantly in their use of the location 'twig', behaviour 'glean' and position 'hang' (six out of six of the tests significant), in their use of the height '0 to 1m' (five out of six tests significant) and in their use of the locations 'branch' and 'herbaceous layer', the substrate 'emerging flower' and the behaviour 'search' (four out of six tests significant). Figures 5.13 and 5.14 summarise the patterns of these significant differences with great tits using the foraging height '0 to 1m', the foraging locations 'branch' and 'herbaceous layer' and the foraging behaviour 'search' more frequently and more than expected than blue tits (Figure 5.13a-d respectively). Blue tits used the foraging location 'twig', the foraging substrate 'emerging flower', the foraging behaviour 'glean' and the foraging position 'hang' more frequently and more than expected than great tits (Figure 5.14a-d respectively).

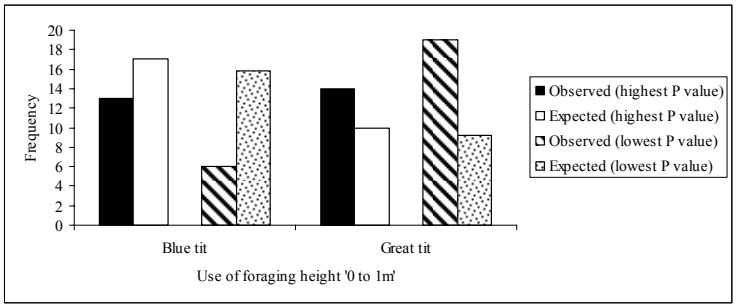
Three out of six of the tests for foraging height '>3m' and for the behaviour 'prey handling' were significant (Table 5.7 c and u), and although not conclusive, this indicated differences between the species. Figure 5.15 outlines these differences with blue tits using the foraging height '>3m' more frequently and more than expected than great tits (Figure 5.15a) and with great tits using the foraging behaviour 'prey handling' more frequently and more than expected than blue tits (Figure 5.15b). Blue tits and great tits mainly did not differ in their use of the categories foraging height '>1m to 3m', foraging locations 'trunk' and 'ground', foraging substrates 'bark', 'bud', 'emerging leaf', 'full leaf' and 'full flower', 'foraging alone', 'foraging with an adult', 'foraging with fledglings', foraging behaviour 'probe' and foraging position 'stand'.

Table 5.7 Two-way G-tests (likelihood ratio test) comparing species (blue tit and great tit) against the observed and expected frequencies of use of various foraging categories. The table shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. N varies between some of the repeated tests due to missing data from some of the individual observations.

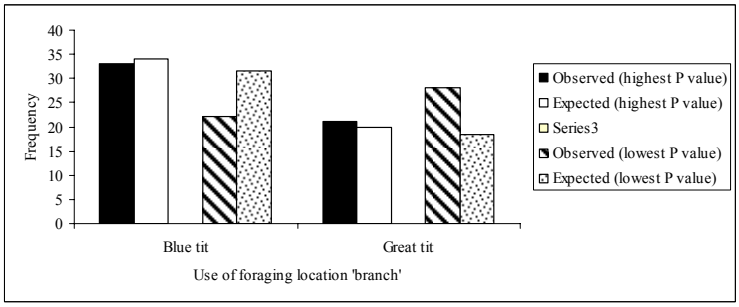
	Test	Number of tests which are significant (out of 6)	*df*	X^2 test of highest P value		X^2 test of lowest P value	
				X^2	N	X^2	*N*
	Species by:						
a)	Height '0 to 1m'	5/6	1	3.037	160	19.021***	160
b)	Height '>1m to 3m'	0/6	1	0.019	160	1.332	160
c)	Height '>3m'	3/6	1	3.342	160	7.375**	160
d)	Location 'trunk'	2/6	1	0.446	160	5.708*	160
e)	Location 'branch'	4/6	1	0.142	160	11.233***	160
f)	Location 'twig'	6/6	1	22.789***	160	48.669***	160
g)	Location 'herbaceous layer'	4/6	1	0.722	159	10.081**	160
h)	Location 'ground'	1/6	1	0.911	159	8.158*	160
i)	Substrate 'bark'	0/6	1	0.280	159	2.645	157
j)	Substrate 'bud'	1/6	1	0.204	159	5.994*	157
k)	Substrate 'emerging leaf'	0/6	1	0.008	159	3.776	157
l)	Substrate 'full leaf'	2/6	1	0.465	157	9.366**	157
m)	Substrate 'emerging flower'	4/6	1	2.309	157	9.458**	159
n)	Substrate 'full flower'	2/6	1	2.848	157	12.572***	159
o)	'Foraging alone'	0/6	1	0.062	160	2.263	160
p)	'Foraging with an adult'	0/6	1	0.001	160	1.289	160
q)	'Foraging with fledglings'	0/6	1	0.077	159	1.488	160
r)	Behaviour 'glean'	6/6	1	9.388**	160	19.445***	160
s)	Behaviour 'search'	4/6	1	2.956	160	15.234***	160
t)	Behaviour 'probe'	1/6	1	0.001	159	4.538*	160
u)	Behaviour 'prey handling'	3/6	1	1.372	160	11.235**	160
v)	Position 'stand'	1/6	1	2.317	146	4.389*	143
w)	Position 'hang'	6/6	1	24.699***	146	64.179***	145

Figure 5.13 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing species (blue tit and great tit) against their use of the foraging categories ‘0-1m’, ‘branch’, ‘herbaceous layer’ and ‘search’. The frequency of non-use of the categories, which was used in the tests to generate the expected values, has been omitted from the graphs for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.7a (‘0-1m’), 5.7e (‘branch’) and 5.7g (‘herbaceous layer’) and 5.7s (‘search’) for the significance levels of these P values.

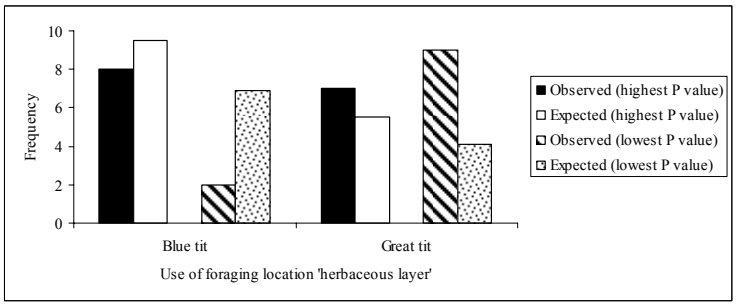
a) Use of foraging height ‘0 to 1m’



b) Use of foraging location ‘branch’



c) Use of foraging location ‘herbaceous layer’



d) Use of foraging behaviour ‘search’

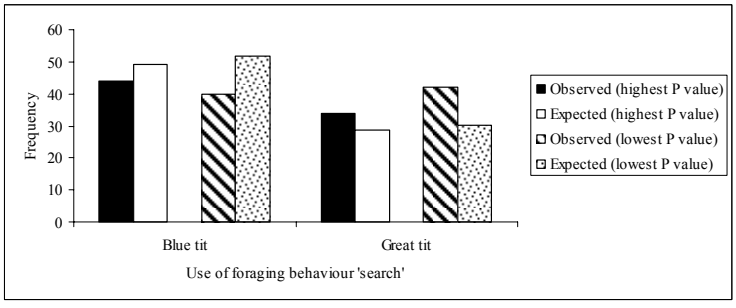
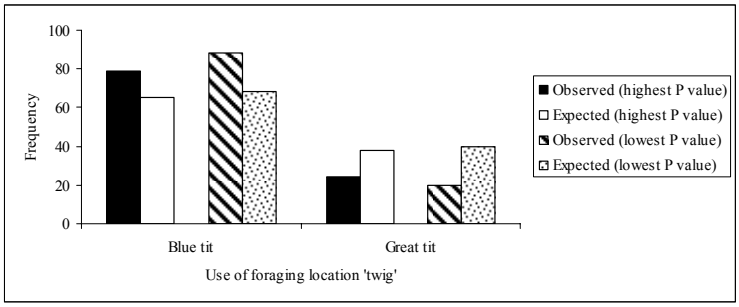
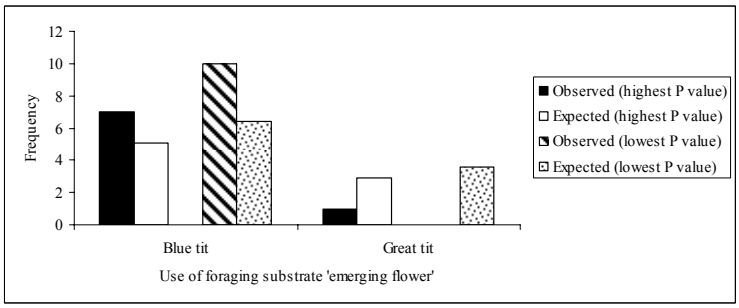


Figure 5.14 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing species (blue tit and great tit) against their use of the foraging categories ‘twig’, ‘emerging flower’, ‘glean’ and ‘hang’. The frequency of non-use of the categories, which was used in the tests to generate the expected values, has been omitted from the graphs for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.7f (‘twig’), 5.7m (‘emerging flower’), 5.7r (‘glean’) and 5.7w (‘hang’) for the significance levels of these P values.

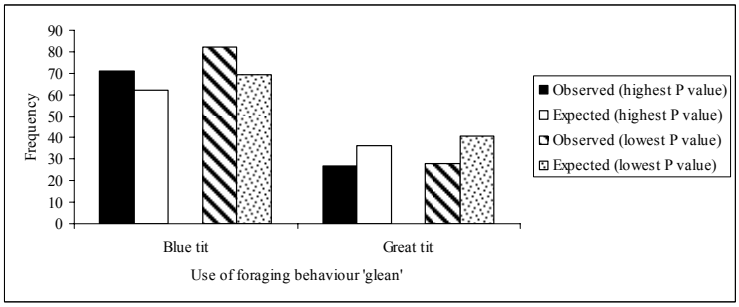
a) Use of foraging location ‘twig’



b) Use of foraging substrate ‘emerging flower’



c) Use of foraging behaviour ‘glean’



d) Use of foraging position ‘hang’

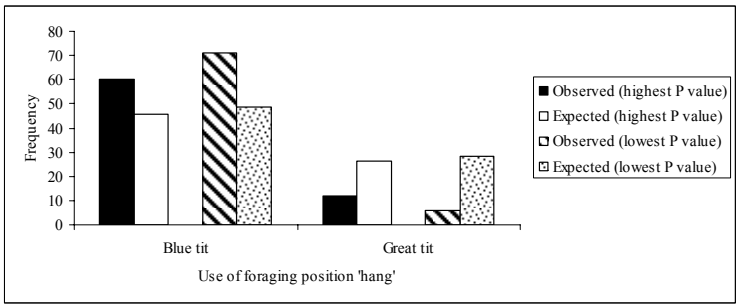
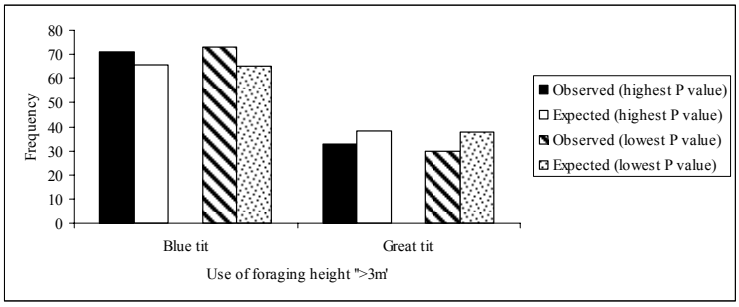
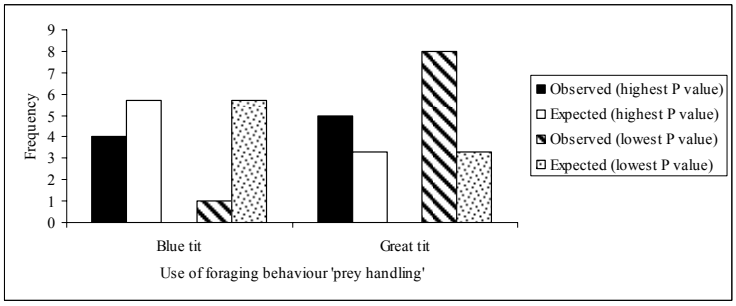


Figure 5.15 Observed and expected frequencies generated from two-way G-tests (likelihood ratio test) comparing species (blue tit and great tit) against their use of the foraging categories '>3m,' and 'prey handling'. The frequency of non-use of the categories, which was used in the tests to generate the expected values, has been omitted from the graphs for clarity. The figure shows the results of the highest and lowest P values obtained from six repeated tests, with each test using an individual bird selected by a different random number. See Table 5.7c ('>3m') and 5.7u ('prey handling') for the significance levels of these P values.

a) Use of foraging height '>3m'



b) Use of foraging behaviour 'prey handling'



5.4 Discussion

Blue tits and great tits were shown to differ in their foraging behaviour with great tits using a wider range of foraging heights and different foraging locations and capture techniques. These species have coevolved for co-existence, and feeding habits are expected to differ (e.g. Alatalo *et al*. 1987; Hartley 1953; Hino *et al*. 2002; Lack 1971). However, in the artificial environment of the CUBG prey availability was likely to differ from that in more 'natural' habitats and thus there are consequences of these respective feeding habits. Tits have been shown to use trees that are suited to their morphological traits and feeding habits, usually determined by the tree foliage (Park 2005). In the CUBG, some patterns existed showing different foraging techniques in different tree taxa, supporting this idea, but these patterns were weak. Overall in the CUBG, habitat structure, which has been shown to affect foraging behaviour (Maurer and Whitmore 1981), appeared to have a greater negative effect on great tit than on blue tit foraging.

5.4.1 Blue tit and great tit foraging behaviours in the CUBG

Blue tits and great tits differed in their foraging heights with blue tits more frequently found at >3m and infrequently found between 0-1m. Although great tits were also found more frequently at >3m than in lower shrub layers or on the ground, they were found feeding at the other heights more than blue tits. This suggests that blue tits are mainly using trees and tall shrubs whereas great tits are foraging lower down in trees, shrubs and herbaceous layers. Other authors detailing tit feeding stations in woodland have also found great tits to feed lower than blue tits in the breeding season (Gibb 1954; Hartley 1953; Lack 1971). However, blue tits were observed foraging at lower heights than reported in these studies, reflecting the available habitat in the CUBG. Blue tits may

also have been found foraging lower down due to observer bias; those foraging higher up may have been more difficult to locate in the tallest trees and so observations were missed. However, in practice the birds were usually located by sound and even when high up in trees they could be heard and then located with binoculars.

For foraging locations, blue tits mainly used twigs whereas great tits used both twigs and branches equally. This is in contrast to other studies where great tits have been found to use branches more frequently (e.g. Gibb 1954; Hartley 1953; Kwok 2009; Lack 1971). In fact Gibb (1954) found that in oak woodland great tits seldom used twigs at all. Branches have also been described as better foraging sites for great tits because twigs make perching difficult for this relatively heavy species (Unno 2002). Blue tits also have the added advantage of being able to hang from twigs, which in the CUBG they did as frequently as they stood upright to capture prey. Great tits however in the CUBG rarely used the foraging position 'hang', which has been described as an energy expensive manoeuvre for them (Park *et al*. 2008; Unno 2002). So although they may be using twigs in the CUBG as frequently as branches, they may not be able to perform effective manoeuvres on twigs in order to capture prey efficiently. Similarly, Rytkönen and Krams (2003) argue that great tits that shifted their foraging behaviour to that of a blue tit, using thinner branches, in a food poor forest, obtained little beneficial effect on breeding success mainly due to morphological constraints.

The fact that blue tits used standing and hanging positions in the CUBG equally, whereas in woodland they have been shown to use hanging more frequently (Partridge 1976), shows an ability to exploit the wide variety of tree and shrub species in the CUBG and shows a greater flexibility than great tits. Different plant taxa may require different foraging positions for the most effective prey detection and capture (Unno 2002) and hanging, although energy expensive may be more efficient, as caterpillar prey

is often found on the undersides of leaves (Greenberg and Gradwohl 1980; Holmes and Schulz 1988). Like great tits, other tits, such as the crested tit (*Lophophanes cristatus*), have also been shown to be restricted in their foraging abilities compared to blue tits (Barluenga *et al*. 2003; Moreno *et al*. 2001).

However, neither blue tits nor great tits used hovering (behaviour of 'other' – see methods) often as a technique to catch prey in the CUBG and this is probably due to morphological constraints, possibly as a consequence of specialisation for feeding in broad-leaved trees (e.g Partridge 1979). It has been argued that species that catch prey primarily by perching or hanging (described by these authors as 'gleaner' species) are more affected by tree species composition and foliage structure than hovering species (Holmes and Robinson 1981). These authors found that 'gleaners' find it easier to use a tree with leaves tight together so they can search many leaves at once whilst hanging or perching; usually these birds have specific tree species preferences. A hoverer on the other hand can quickly fly along a branch on any type of tree and so is less tree species specific. So both blue tits and great tits in the heterogeneous vegetation of the CUBG may be at a disadvantage morphologically by not being able to easily hover but again great tits are probably even more disadvantaged by mainly being constrained to using the technique of standing.

Great tits and to a lesser extent blue tits were found foraging in the herbaceous layer in the CUBG. This is in contrast to studies in woodland where over a whole year blue tits used herbaceous layers only 1% of the time and great tits 4% of the time (Gibb 1954): these percentages are likely to be even lower during the breeding season when both species are argued to shift to caterpillar prey in trees (Hartley 1953; Lack 1971). Also Kwok (2009) never found great tits using understory plants and leaf litter in his study. The use of the herbaceous layers in the CUBG therefore may indicate a lack of food in

preferred locations and a shift to other foraging substrates, which, although not usually used, may be more freely available but at the same time may contain little appropriate invertebrate prey (see Chapter 2 for herbaceous layer availability).

For foraging behaviours, great tits were found to search more than they gleaned and blue tits gleaned more than they searched. This may indicate that great tits find it more difficult to forage in the CUBG and have less success at finding and 'gleaning' prey. Great tits have been shown to be highly selective for large prey (Naef-Daenzer and Keller 1999; Naef-Denzer *et al*. 2000) and so may be 'searching' more in the CUBG for larger prey items than blue tits, which may pick off smaller and possibly more abundant prey items by using more diverse techniques. Also, Hino *et al.* (2002) found that great tits used trees with the highest total invertebrate biomass, searching only a few tree species and argued that this is the best strategy for inflexible perch gleaners. Although selectivity of prey has been shown to coincide with higher chick masses in blue tits (Stauss *et al*. 2005), with such a wide variety of trees with differing invertebrate abundances in the CUBG great tits may be unable to use this strategy successfully. They may be unable to select the 'best' vegetation with high invertebrate biomass due to this heterogeneity and thus their increased searching may reflect this inability.

5.4.2 Foraging behaviours between breeding periods

Both blue tits and great tits show a shift in the location of foraging from early in the season during the nest building/egg laying/incubation period, to the chick feeding and fledging periods. There are changes in the options available, for example 'full leaves' becoming progressively more available through the season. However, in the CUBG there is an abundance of evergreen and semi-evergreen plants available, which have full leaves that could be used, and the observation that birds use 'full leaves' significantly

more in later periods of nesting may therefore reflect the bird's preferences for deciduous leaves (Lack 1971; Partridge 1979; Perrins 1979).

The test for use of the substrate 'full flower' between breeding periods, showing blue tits using flowers most frequently in the nest building/egg laying/incubation period, may also be subject to the same biases of availability mentioned above for 'full leaf'. However, due to the heterogeneous nature of the CUBG there is a wide spread of flowering times over the whole breeding period. Different trees and shrubs, even within genera have different flowering times, for example *Acer campestre* doesn't start flowering until May and flowers until June whereas *Acer pseudoplatanus* starts flowering in April and has flowers until May (Fitter and Peat 1994). Flowers of the herbaceous plant cow parsley (*Anthriscus sylvestris*) in the CUBG also offered foraging opportunities to blue tits and great tits in the two latter breeding periods. So, despite flowers being available in the CUBG during all breeding periods, blue tits used them frequently in the nest building/egg laying/incubation period but relatively infrequently during the chick feeding and fledging periods. This may again point to a switch to using full leaves during the latter two periods where suitable chick prey such as caterpillars are more likely to be feeding (Lack 1971). Additionally, flowers may only house small prey items such as midges (e.g. Roskam and Uffelen 1980), which may be suitable prey for the adults, but inappropriate for the chicks. Great tits however didn't differ in their use of flowers throughout the breeding periods and in fact used flowers overall relatively infrequently. This may again be related to the size of prey items, which if relatively small may be too small to be of nutritious value to the great tit which prefers larger prey than blue tits (Nour *et al*. 1998). Blue tits have also been shown to feed on nectar early in the breeding season (Fitzpatrick 1994; Kay 1985; Perrins 1979; Thompson *et al*. 1996), which may be a highly profitable food source for this smaller tit

species but not so for the larger great tit. Moreover, flowers, often being on the ends of twigs, may be relatively inaccessible to the great tit.

5.4.3 Foraging behaviours associated with different genera of trees

Differences were found between the foraging behaviours of blue tits and great tits on different genera of trees, although there are certain problems with these tests which will be discussed below. In general, blue tits were found to forage more frequently on the flowers of *Betula* and, to a lesser extent, *Prunus* than on the flowers of *Acer* and *Quercus*. Great tits foraged on the full leaves of *Prunus* more than on full leaves of *Acer*.

It is perhaps not surprising that blue tits foraged on the flowers of *Betula* most frequently; Gibb (1954) also found blue tits using birch catkins early in the breeding season and the catkins may be suitable foraging substrates for blue tits due to their ability to reach them by hanging. This may also explain why great tits, which were found to hang infrequently, are not observed feeding in birch to the same extent. The prey obtained from birch catkins are likely to be small, such as midges (e.g. Roskam and Uffelen 1980), i.e. too small for this larger species. Also, as mentioned above, blue tits have been documented using flowers as a source of nectar (Fitzpatrick 1994; Kay 1985; Perrins 1979; Thompson *et al*. 1996) and so may be using the birch catkins for this reason.

However, this finding also highlights the potential problems with this test. The flowers of the different plant taxa tested may be available at different times of the breeding season, and, as shown both in this study and others (Gibb 1954; Lack 1971), blue tits move to leaves when they are feeding their chicks. Flowers are therefore mainly used in

the nest building/egg laying/incubation periods, which is mainly when the *Betula* and *Prunus* flowers were available. The chi-square tests assumed that flowers were more or less available to the tits throughout the whole breeding season but because the phenology of both flowers and leaves of different tree species may differ in time and space these assumptions of equal availability of substrates may not have been met. Differences found in foraging on flowers of different genera may not be a reflection of species preferences. It may instead reflect the relative abundance of the tree species with flowers. In the extremely heterogeneous environment of the CUBG, the availability of flowers, buds, and/or leaves is constantly changing and not readily represented in the expected values of the statistical tests. The most convincing patterns emerged for the trees that are the more abundant and less isolated, such as *Betula.*

5.4.4 Conclusion

Blue tits and great tits have been shown to differ in their foraging abilities in the CUBG and it appears that feeding techniques may be less effective in habitat to which a bird is not adapted (Partridge 1976). Both species are adapted morphologically to broadleaved deciduous woodland (Lack 1971; Suhonen *et al.* 1994) yet blue tits, the lighter and more agile of the two species, appeared to be more effective at foraging in the wider variety of plants available in the heterogeneous vegetation of the CUBG. Great tits however, being constrained by their size (which affects both foraging behaviour and prey suitability/selection) and morphology (e.g. Moreno and Carrascal 1993), appeared to lack the ability to forage as effectively as blue tits across the different plant species available. Both species were observed feeding lower, and using herbaceous layers more frequently than reported previously (Gibb 1954; Kwok 2009). This may be an attempt at adaptation due to the apparent lack of suitable trees. However, given the poor breeding success of both species compared to woodland (Chapter 4), if this is an attempt at

adaptation it does not appear to be working; to differing extents both species suffer from ineffective foraging in this urban garden.

CHAPTER 6

General conclusions

6.1 Introduction

As urbanisation increases wildlife conservation in urban habitats has become increasingly important. Urbanisation can have detrimental effects on prey availability due to an abundance of exotic flora, changes in the predator community and habitat fragmentation (reviewed in Chace and Walsh 2006). The aim of this thesis was to explore the relationships between blue tit (*Cyanistes caeruleus*) and great tit (*Parus major*) breeding success and habitat composition and structure in a large urban garden and to relate this to the consequences, in terms of invertebrate availability for their chicks, of foraging in a habitat that contains an abundance of exotic flora.

6.2 Key findings

Exotic vegetation has been shown to be poor in insect species richness and abundance compared to native vegetation (Southwood *et al.* 1982; Sugiura 2010; Tallamy and Shropshire 2009). However, in this thesis it has been shown that blue tits and great tits differ in their reproductive success in the CUBG, an urban garden with an abundance of exotic flora. This may be partly due to different responses in their foraging preferences, behaviours and techniques in the CUBG, which affects their ability to both find and capture prey successfully. Both species have lowered reproductive success compared to other habitats including woodland and marginal habitats with native vegetation, but great tits appear to do worse than blue tits, rearing lower quality chicks in terms of mean

mass. Blue tits appear to have adopted a better foraging strategy by preferentially choosing native deciduous trees over the abundance of non-natives available in the CUBG and their morphological adaptation, enabling them to exploit a wider variety of foraging substrates, especially thin twigs and leaves in the outer canopy, may facilitate better use of such resources.

In contrast, great tits, being the larger and less agile of the two species, may not be able to cope with low abundances of native flora. Great tits have, for example, been shown to prefer foraging in a small selection of tree species with high invertebrate biomass (Hino *et al*, 2002) and may become non-selective given an overwhelming choice of a large variety of plant species with potentially low invertebrate biomass and consequently low prey encounter rates (e.g. Krebs *et al*. 1977).

Although blue tit and great tit populations in the UK are not under threat (Amar *et al*. 2006; Eaton *et al*. 2009; Hewson *et al*. 2007), the fact that these two closely related species differ in their reproductive and foraging abilities in the CUBG may highlight potential problems for productivity and recruitment in the future if urbanisation continues increasing at a fast rate. It has been argued for example that the decline of the house sparrow (*Passer domesticus*) is due to their inability to produce enough young to sustain the population and that this in turn is related to inappropriate habitat and low invertebrate food availability in highly urbanised areas (Vincent 2006). The poor breeding success of blue tits and great tits in urban environments (e.g. Hinsley *et al.* 2008, 2009; Chapter 4 of this thesis) suggests that they may be affected similarly to the house sparrow due to low invertebrate abundance. In fact various studies of urban birds have noted that the species most likely to disappear as urbanisation increases are small arboreal insectivores (Beissinger and Osborne 1982; Clergeau *et al*. 1998; Crooks *et al*. 2004). However, blue tit and great tit populations, unlike the house sparrow are

increasing in the UK (Amar *et al*. 2006; Eaton *et al*. 2009; Hewson *et al*. 2007). The key difference between the house sparrow and the two tit species may be that house sparrows are a colonial species and increased isolation of sparrow sub-populations may have resulted in small breeding colonies dying out because they don't produce enough recruits and/or don't receive enough immigrants to keep them going (Summers-Smith 2003). Sparrows have also declined on farmland (Summers-Smith 2003) so the pool of potential dispersers to move into urban areas may also have declined. Blue tits and great tits on the other hand are not under threat in other habitats so the increased pool of potential dispersers into urban areas may explain why they still maintain their numbers in urban areas despite the poor breeding success. I will discuss populations and dispersal of blue tits and great tits in more detail below (section 6.3). This research highlights how the degradation of non-urban habitats due to increased urbanisation may lead to the decline of species, including blue tits and great tits, in urban habitats. Therefore it is important that the continual urbanisation is offset by the addition of appropriate foraging habitats.

However, what may be an appropriate foraging habitat for one species may not be the same for another, again as highlighted by the differences found in this study of blue tits and great tits abilities to forage successfully in urban environments and the impact this has on their breeding. It is therefore important to address the needs of a wide variety of insectivorous passerines by studying which tree species compositions and habitats would benefit the majority of bird species and then offer recommendations for landscape management. Other taxa respond differently to structure and composition and so the addition of certain tree species may be advantageous to some birds but not to others. For example, house sparrows would benefit from the addition of grassy areas and deciduous shrubs due to aphids and spiders being abundant in these habitat types (Vincent 2006). Blue tits and great tits however would benefit more by the addition of

native deciduous trees, such as oaks, that house an abundance of caterpillar prey (Hinsley *et al*. 2008, 2009).

6.3 Why do birds choose to breed in food poor habitats?

In Chapter 4 it has been argued that both blue tits and great tits, despite producing a smaller clutch size in the CUBG, needed to produce a clutch size even smaller in order to feed their broods successfully with the lowered food supply. Chapter 1 explored avian breeding ecology and maladaptive clutch sizes, and outlined Lack's (1958) argument that these maladaptations happen due to the tit population not being genetically isolated and thus unable to evolve an appropriate response to the food supply. This argument would also fit with the foraging constraints of blue tits, and more so great tits, in the CUBG seen in Chapter 5 where they are morphologically less able to forage as successfully in altered habitats as in those where they evolved (e.g. see Partridge 1976). Although blue tits appear to do better reproductively than great tits in the CUBG, breeding success of both species could be better if they chose to breed in food rich habitats and habitats that contain appropriate foraging substrates. So why do some choose to breed in food poor urban habitats? Urbanisation and habitat modification is likely to continue increasing for the foreseeable future (see review in Chamberlain *et al*. 2009) so it may not be so much of a 'choice' to breed in poorer habitats but more to do with their preferred habitats becoming increasingly less available and fragmented. This could result in a 'sink' population which can only be sustained by immigration from better quality 'source' habitats (such as deciduous woodland) (Blondel *et al*. 1993, 2001, 2006; Dias 1996). Dias (1996) argues that reproduction is poor in lower quality habitats and that these 'sink' habitats are usually dominated by subordinate individuals (those having 'phenotypically lower fitness')

which are maladapted to their environment due to continual gene flow from source populations.

However, whether or not the CUBG and urban habitats in general are 'sink' populations is a complex issue and requires further investigation including exploring urban tit life histories. Although poor breeding success of blue tits and great tits in urban environments is common and is probably due to poor chick food availability during the breeding season (Chamberlain *et al*. 2009), adult winter survival may be better than in 'higher quality' breeding habitats and this represents a classic trade off. If tits can survive longer, having fewer recruits per year, but spread this over a greater number of breeding seasons, their overall lifetime reproductive success may be better or similar in urban environments than in other habitats. Their over winter survival in urban habitats may for example be helped by warmer temperatures (Chace and Walsh 2006), anthropomorphic food (Jokimäki *et al*. 1996; Robb *et al*. 2008b) and possibly in the CUBG by a glut of food from the wide variety of trees that may offer a wider variety of seeds, nuts and fruit in the winter than in other habitats, where they often rely on beechmast (Perrins 1966, 1979; van Balen 1980). Also the continual presence of humans throughout the day may limit opportunities for predation due to avoidance behaviour (Chace and Walsh 2006) and some studies have found nest predation to decrease as urbanisation increases (e.g. Gering and Blair 1999). Urban environments may therefore offer a 'safe haven' for breeding tits. Certainly in Wicken Fen, where human activity was minimal compared to the CUBG, the boxes were heavily predated by weasels (*Mustela erminea*) (pers. obs.). A weasel was seen in the CUBG but there have been no known incidences of predation on any of our nest boxes by this species (pers. obs.). In the CUBG, there are other potential predators, namely great spotted woodpeckers (*Dendrocopos major*), jays (*Garrulus glandarius*), magpies (*Pica pica*), grey squirrels (*Sciurus carolinensis*) and sparrowhawks (*Accipiter nisus*) (one pair

known), but their impact appears to be minimal on the breeding tit population, whilst they are in nest boxes at least (pers. obs.). Additionally, the comparison of chick mean masses between the sites in Chapter 4, which uses data for chicks at 11 days of age, does not take into account actual fledging date. It could for example be that urban birds spend longer in the nest than woodland birds, which may result in their mean masses being higher at fledging than would be expected when they were originally weighed at day 11. Having a larger mean mass at fledging may increase their chances of future survival (Cichon and Lindén 1995; Naef-Daenzer *et al*. 2001; Perrins 1965; Perrins and McCleery 2001). Some evidence has recently been published arguing that urban populations are not necessarily sink populations (Björklund *et al* 2010). These authors showed that genetic differences in great tits were evident between 12 parks in Barcelona, that relatedness within parks was high and that mortality was low. Additionally, gene flow was higher from the town to a nearby forest and not vice versa, which would be expected in a sink population. This suggests that the parks may represent individual, self sustaining populations that are not dependent on immigrants from the forest source and that although reproductive success is poor, the low mortality means reproduction is spread over more breeding seasons.

However, urban environments may not always result in low mortality for all passerines. Although blue tits and great tits don't appear to be heavily predated in the CUBG and therefore may have lower mortality, open nesting bird species in the CUBG such as blackbirds (*Turdus merula*), may not be so protected, especially in the case of predation by the high numbers of corvids present (mainly jays and magpies) (Chace and Walsh 2006; Robb *et al*. 2008a). Additionally, the use of human erected bird feeding stations may have negative consequences for small passerine mortality due to increased predation risk from birds of prey and disease spread (reviewed in Chace and Walsh

2006). Feeders may also act as ecological traps giving birds inappropriate cues as to the levels of natural food available during the breeding season (Robb *et al*. 2008a).

6.4 Future research into urban environments

Few studies have looked at the link between breeding success of tits in urban environments and the impact that floral composition and origin and substrate structure may have on their foraging abilities. This thesis provides insights into the ecological differences and similarities of blue tit and great tit feeding ecology during the breeding season and the relationships between this and their reproductive success. The CUBG however represents just one example of an urban garden and so only tentative conclusions can be made until further work in other urban environments can be used to corroborate these findings. In fact, in lieu of this, nest boxes have been placed in other urban areas of Cambridge, including a council run park to the South of Cambridge, Cherry Hinton Hall.

In the CUBG, measuring over winter survival, population changes and demography of blue tits and great tits was difficult as only a small number of chicks appeared to be recruited to the population. I say 'appeared' because as the CUBG is surrounded by residential gardens the CUBG itself did not represent the whole population. It was difficult to establish whether chicks fledging from the boxes within the CUBG went on to breed just outside of the gardens, emigrated further or did not survive at all. There is certainly an influx of birds during winter, when they are colour ringed for the next breeding season and a large number of these winter birds do not go on to breed in the CUBG (see Appendix). This could suggest the CUBG is a 'sink' population with a continual influx of immigrants. However, a large number of CUBG blue tits and great tits do go on to breed through successive seasons (see Table 2 for blue tits and Table 5

for great tits of the Appendix) suggesting low mortality in this urban environment. Future work could therefore include recapture work in the surrounding residential areas to try to establish a better measure of survival rate and life histories of urban tits and to compare these to other sites, where reproduction is better per season, and to other urban sites such as Cherry Hinton Hall. Genetic work could also be undertaken to explore relatedness within the gardens and genetic differentiation between urban populations across Cambridge.

Throughout much of this thesis, reference has been made to exotic and evergreen plants being invertebrate poor and that the main limiting factor on breeding success in the CUBG is mainly due to this poor food supply. This warrants further investigation to establish the actual diet that is being fed to the chicks and to see if caterpillars are underrepresented. As I mentioned in the Chapter 3 discussion, current investigations to analyse chick faecal sacs and video footage from the nest boxes will offer insights into this topic. Additionally, it would also be interesting to analyse adult diet during the winter to see if the CUBG offers any food rich foraging substrates that may benefit over winter survival.

6.5 Conclusion

Blue tits and great tits have been extensively studied over the years and a number of theories surrounding avian breeding ecology have been established using data collated from these studies, almost exclusively conducted in woodland (see Chapter 1 for a review). As urbanisation is only likely to continue to increase (more people now live in cities than in rural areas, UNFPA 2007) and consequently lead to the loss of natural habitats such as woodland, new approaches such as the ones outlined in this thesis, are

needed to assess the impacts that these urban environments are having on bird populations and, if needed, to encourage conservation measures sooner rather than later.

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APPENDIX

Blue tit population data

Table 1 Population data of blue tits in the CUBG showing numbers and ages of individuals colour ringed between winter 2005-spring 2008. Data is split down into ringing periods (periods of ringing that precede the following breeding season) and breeding seasons (2006-2008).

		Numbers colour ringed (inluding retraps)				Age (of individuals colour ringed)			
Ringing period	Breeding season	New	Retraps (from previous season(s) (excludes any recruits that were ringed as chicks)	Recruits (any chicks ringed in previous season(s))	Total	Juvenile / first year after hatching	Adult	Unknown age	Number (out of those ringed/retrapped during the associated ringing period) observed foraging in the CUBG during the associated breeding season
Winter 2005/2006	2006	43	4	1	48	21	27	0	29 (60%)
Winter 2006/2007	2007	29	11	4	44	30	14	0	29 (66%)
Winter 2007/ 2008	2008	33	11	2	46	28	18	0	28 (61%)

Table 2 Population data of blue tits in the CUBG showing numbers and ages of known colour ringed individuals breeding in nest boxes between 2006-2008. * 'unknown colour ring' refers to individuals that failed to be identified at the nest box.

		Number of birds breeding in nest boxes				Age of birds breeding in nest boxes		
Ringing period	Breeding season	Number of birds colour ringed in associated ringing period	Number of birds colour ringed in previous ringing period(s)	Number of birds with no colour ring or unknown colour ring *	Total breeding in boxes	First year after hatching	Adult	Unknown age
Winter 2005/2006	2006	18	9	3	30	6	21	3
Winter 2006/2007	2007	12	14	6	32	11	15	6
Winter 2007/ 2008	2008	13	14	1	28	11	16	1

Table 3 showing the total number and ages of blue tits seen foraging in the CUBG in the associated breeding season (2006-2008). This includes birds that may not necessarily have been trapped in the ringing period preceding the associated breeding season.

		Number of individuals with colour rings observed foraging		Age of foragers		
Ringing period	Breeding season	Number of foragers ringed in previous ringing period(s)	Total number	First year after hatching	Adult	Unknown age
Winter 2005/2006	2006	22	48	8	39	1
Winter 2006/2007	2007	29	50	18	32	0
Winter 2007/ 2008	2008	20	39	14	25	0

Table 4 Population data of great tits in the CUBG showing numbers and ages of individuals colour ringed between winter 2005-spring 2008. Data is split down into ringing periods (periods of ringing that precede the following breeding season) and breeding seasons (2006-2008).

		Numbers colour ringed (inluding retraps)				Age (of individuals colour ringed)			
Ringing period	Breeding season	New	Retraps (from previous season(s) (excludes any recruits that were ringed as chicks)	Recruits (any chicks ringed in previous season(s))	Total	Juvenile / first year after hatching	Adult	Unknown age	Number (out of those ringed/retrapped during the associated ringing period) observed foraging in the CUBG during the associated breeding season
Winter 2005/2006	2006	20	8	0	28	7	19	2	18 (64%)
Winter 2006/2007	2007	20	5	2	27	9	16	2	21 (78%)
Winter 2007/ 2008	2008	11	7	1	19	9	10	0	11 (58%)

Table 5 Population data of great tits in the CUBG showing numbers and ages of known colour ringed individuals breeding in nest boxes between 2006-2008. * 'unknown colour ring' refers to individuals that failed to be identified at the nest box.

		Number of birds breeding in nest boxes				Age of birds breeding in nest boxes		
Ringing period	Breeding season	Number of birds colour ringed in associated ringing period	Number of birds colour ringed in previous ringing period(s)	Number of birds with no colour ring or unknown colour ring *	Total breeding in boxes	First year after hatching	Adult	Unknown age
Winter 2005/2006	2006	10	6	6	22	0	15	7
Winter 2006/2007	2007	17	7	2	26	5	17	4
Winter 2007/ 2008	2008	8	9	3	20	15	2	3

Table 6 showing the total number and ages of great tits seen foraging in the CUBG in the associated breeding season (2006-2008). This includes birds that may not necessarily have been trapped in the ringing period preceding the associated breeding season.

		Number of individuals with colour rings observed foraging		Age of foragers		
Ringing period	Breeding season	Number of foragers ringed in previous ringing period(s)	Total number	First year after hatching	Adult	Unknown age
Winter 2005/2006	2006	15	25	0	24	1
Winter 2006/2007	2007	13	30	7	21	2
Winter 2007/ 2008	2008	16	22	5	17	0

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